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CANINE OBJECT PERCEPTION STUDIED WITH NON-INVASIVE ELECTROENCEPHALOGRAPHY AND EYE GAZE TRACKING

-A COMPARATIVE PERSPECTIVE

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DOCTORAL DISSERTATION

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ABSTRACT

Canine cognition has been widely studied especially with behavioral methods. Behavioral studies have shown that dog's social cognitive abilities are similar to preverbal human infants, and that dogs are excellent readers of human communicative gestures. However, behavioral studies cannot determine the cognitive processes and neuronal functions underlying the behavior. In addition, direct comparisons between humans and dogs, highlighting differences and similarities between the species, have been rarely used in previous studies. The aim of this thesis was to evaluate the feasibility of two novel non-invasive methods of examining dog social cognitive functions, and also to compare human and dog cognitive abilities with eye gaze tracking.

The feasibility of non-invasive electroencephalography (EEG) and eye gaze tracking in dog cognitive studies were studied in experiments I–IV. In an EEG experiment, the visual event-related potentials (ERPs) were measured while dogs were watching human and canine facial images. In the eye tracking experiments fixations and saccades towards the stimulus images were measured.

Experiment I confirmed, for the first time, the usability of completely non-invasive EEG measurement in intact fully alert dogs. The early visual ERPs were detected at 75–100 ms from the stimulus onset. In Experiments II–IV, remote eye gaze tracking was used to study visual cognitive abilities in dogs. The experiments verified the feasibility of the eye tracking method in dogs and showed that dogs' attention was focused on the informative areas of the images. Experiment II showed that dogs preferred facial images of dogs and humans over inanimate objects. In experiment III, comparisons between the eye movements of humans and dogs revealed that both dogs and humans gazed longer social interaction images than non-social images. However, dogs gazed longer human interaction images and humans gazed longer at dog interaction images, which indicates that processing social interaction of another species might take more

time. Also in experiment III, family dogs gazed at images longer than kennel dogs, suggesting that kennel dogs' limited social environment might have affected their processing of social stimuli. Experiment IV explored dogs' gazing behavior towards natural images containing dogs, humans and wild animals. This study showed that dogs focused their gaze at living creatures and especially gazed at the biologically informative areas in the images, such as the head area.

In conclusion, EEG and eye tracking are promising methods for studying dog cognition, and eye tracking can be used to compare responses between humans and dogs. EEG and eye tracking studies showed that dogs were focusing on the objects in the images and their gazing behavior depended on the image category. These studies highlight the importance of facial information to dogs, and also reflect their excellent skills in comprehending social and emotional cues in both conspecifics and non-conspecifics.

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications, which are referred to by their roman numerals in the text.

I **Törnqvist H**, Kujala MV, Somppi S, Hänninen L, Pastell M, Krause CM, Kujala J, Vainio O (2013) Visual event-related potentials of dogs: a non-invasive electroencephalography study. *Animal Cognition* 16, 973–982.

II Somppi S**, Törnqvist H,** Hänninen L, Krause CM, Vainio O (2012) Dogs do look at images -eye tracking in canine cognition research. *Animal Cognition* 15, 163–174.

III **Törnqvist H**, Somppi S, Koskela A, Krause CM, Vainio O, Kujala MV (2015) Comparison of dogs and humans in visual scanning of social interaction. *Royal Society Open Science* 2, 150341.

IV **Törnqvist H,** Somppi S, Kujala MV, Vainio O (*submitted*) Observing animals and humans: dogs target their gaze to the biological information in natural scenes.

ABBREVIATIONS

AOI	area of interest
CRT	cathode ray tube
CT	computed tomography
EEG	electroencephalography
ERP	event-related potential
fMRI	functional magnetic resonance imaging
fNIRS	functional near-infrared spectroscopy
IRT	infrared thermography
LCD	liquid-crystal display
LGN	lateral geniculate nucleus
ToM	theory of mind

1 INTRODUCTION

Dogs have lived alongside people for approximately 18 000–32 000 years (Thalmann et al. 2013) and during that time they have evolved forms of human-like social cognition, that differentiate their behavior and responses from those of wolves (Miklósi and Topál 2013). Dogs are more skillful at reading human communicative behavior than wolves that are raised by humans (*e.g.* Hare et al. 2002). During domestication, dogs have adapted to living with humans by developing forms of cognition that enable them to understand human communicative signals (Hare and Tomasello 2005). Because of their human-like social skills, dogs are considered to be one of the best model animals for human social behavior and disorders (Miklósi and Topál 2013; Head 2013). Unlike laboratory dogs or other laboratory animals, family dogs also share the environment and lifestyle with their human counterparts. Comparative studies, where species-specific natural abilities have been considered can provide detailed information about the similarities in processing social and emotional information. However, comparative cognition studies between humans and dogs, where both species are measured with comparable methodology, are still rare.

Examining dog cognition has to be conducted with indirect methods, because unlike humans, dogs cannot tell us directly what they are thinking and how they are feeling. Previously, dogs' cognitive abilities have been extensively studied with tasks that require behavioral responses (for a review, Bensky et al. 2013). Despite the extensive research on canine behavior, still relatively little is known about the mental and neural background behind this behavior. This thesis employed two novel non-invasive methods, EEG and eye tracking, to measure the neural and visual responses associated with object viewing in dogs. The visual ERPs were measured to examine basic visual brain potentials during the image viewing, and also to reveal differences in brain potentials between human and canine facial images (Experiment I).

The eye movements of dogs were measured to assess where dogs focus their attention and to study the effect of image category on the gazing behavior

(Experiments II–IV). In addition, dogs' and humans' gazing behavior was compared during the viewing of social stimuli (Experiment III). Furthermore, the eye movements of two dog populations living in different social environments were compared to evaluate the effect of social environment on canine gazing behavior (Experiments III and IV).

Traditionally, EEG studies in animals have mostly been invasive. To date, there are only a few studies where fully non-invasive EEG methods have been used in conscious dogs in a manner similar to that standardly used in healthy humans (Kujala et al. 2013; Kis et al. 2014; Kis et al. 2017a; Bunford et al. 2018). Other studies published to date have used needle electrodes (Howell et al. 2011, 2012; James et al. 2011, 2017) or other invasive electrodes (Bichsel et al.1988), sedatives (Adams et al. 1987; Berendt et al.1999; Jeserevics et al. 2007; Pellegrino and Sica 2004) or they have measured EEG during sleep (Kis et al. 2014, 2017a; Bunford 2018). In humans, ERP studies are very common, but not in dogs probably due to different research traditions and difficulties in measuring EEG in fully alert dogs. Concurrently with the work of this thesis, great advancements in comparative studies have been made with non-invasive functional magnetic resonance imaging (fMRI) method adapted from human studies. fMRI studies have for example found similarities in the functional anatomy of human and canine brains, *e.g.* related to processing of facial information (*e.g.* Berns et al. 2012; Andics et al. 2014; Dilks et al. 2015). However, it is not fully known to what extent brain structures in dogs anatomically and functionally correspond to those in humans, and whether those structures underpin similar cognitive functions between species (for a review, Bunford et al. 2017).

For dogs, the sense of smell is highly important, but dogs use also their sight to communicate and navigate in their surroundings. For example, many tasks given by humans to dogs require acute eyesight, such as hunting, herding and guarding. Surprisingly little is known about dogs' basic visual abilities, and this makes it difficult to compare visual perception between humans and dogs. Nevertheless, almost all behavioral cognitive studies conducted in dogs are based on vision, although it is not known in detail how dogs perceive these tasks (for a review, Byosiere et al. 2018). By using eye

tracking we acquire millisecond-scale temporal and millimeter-scale spatial information on where dogs focus their attention; in which order or how quickly they attend to different visual features; or how they view different kinds of visual stimuli. Furthermore, eye gaze tracking allows better direct comparisons between canine and human gazing behavior and visual cognition.

This thesis explores the usability of non-invasive EEG and eye tracking in dog cognition studies. The motivation behind the thesis was to develop new animal-friendly methods, and to characterize canine visual cognitive abilities related to social perception of conspecifics and non-conspecifics and subsequently, the underlying mechanisms involved. We hypothesized that dogs' neurophysiological brain potentials can be detected non-invasively from the surface of the skin and that the early visual event-related responses can be measured (Experiment I). In addition, we expected that dogs focus their attention to the biologically relevant areas of images, such as the head/ face area (Experiments II–IV), and that image composition affects the dogs' gazing behavior (Experiment IV). Furthermore, we anticipated that dogs' gazing times differ between image categories, and that they prefer conspecific images over other image categories (Experiments II–IV).

2 REVIEW OF THE LITERATURE

2.1 COMPARATIVE COGNITION

Cognition refers to the mechanisms of processing, acquiring, storing and acting on information, and it includes different cognitive processes such as perception, learning, memory and decision making (Shettleworth 2010). Comparative studies between humans and animals have a long history; already Darwin (1859, 1872) proposed that humans and non-human animals share similarities in anatomy, emotions, and cognitive abilities. As humans, we have the greatest understanding of our own cognitive abilities, and comparative cognitive studies often examine the abilities of non-human species in situations that humans are able to solve. In the traditional approach for studying the evolution of human social cognition, comparisons have been made between non-human primates and humans (*e.g.* Seed and Tomasello 2010). But the last 20 years has seen a substantial increase in canine behavior and cognition studies for several reasons. Dogs' trainability and willingness to cooperate with humans makes them not only great companions and working partners in a variety of jobs, but also excellent study subjects.

There are similarities in dogs' and children's responsiveness to communicative cues, and dogs' performance appears comparable to 2–3-year-childrens' performance, although this is dependent upon the type of skills tested (Kaminski et al. 2004; Virányi et al. 2006; Lakatos et al. 2009; Racca et al. 2012; Gergely et al. 2019). Despite increasing interest in comparative studies, there are only a few studies where the cognitive functions of adult humans and dogs have been directly compared by utilizing similar research methods (Kis et al. 2014; Andics et al. 2014; Correia-Caeiro et al. 2020).

2.2 NEURONAL BASIS UNDERLYING DOG COGNITIVE FUNCTIONS

Dogs have become a popular research animals in behavioral and cognitive studies, but for some reason little research has been conducted on the canine brain in the last decades. The primary animal models in comparative cognitive neuroscience have been non-human primates, rodents, and birds (*e.g.* Perretta 2009; Vandamme 2014; Clayton and Emery 2015). Many people may find invasive research of the canine brain ethically unacceptable, because dogs hold a privileged status as pets in Western society (Berns and Cook 2016).

All mammals have highly developed right and left cerebral hemispheres, which together constitute the cerebrum (Etsuro 2016). The cerebral hemispheres consist of the cerebral cortex (*i.e.* the gray matter at the surface of the cerebrum), white matter and basal nuclei. Each cerebral hemisphere has five cerebral lobes: the temporal, frontal, parietal, occipital and piriform. These cerebral lobes have rather arbitrary boundaries in dogs, because there is great variation in the sulci and gyri patterns (inward and outward folds of the cerebral cortex), which makes it difficult to outline clear borders of the cerebral lobes. Nevertheless, a few distinct sulci commonly found in dogs serve as reference points for a description of the cerebral lobes (Etsuro 2016).

Dogs and humans have differences in skull formation and accordingly in brain anatomy. Also the breeding of dogs to produce specific breeds has affected the form of their brains. In general, the size of the dog brain is smaller than that of the human brain (see Figure 1). In dogs the cerebral cortex is less gyrificated (folded) containing fewer neurons than in humans, who have the most developed cerebral cortex (Roth and Dicke 2005; Kaas 2013). The cerebral cortex is a central region controlling complex cognitive behaviors in mammals (Kaas 2013; Geschwind and Rakic 2013), and it has been suggested that the absolute number of neurons in the cerebral cortex is a major determinant of the cognitive abilities (Roth and Dicke 2005; Herculano-Houzel 2017).

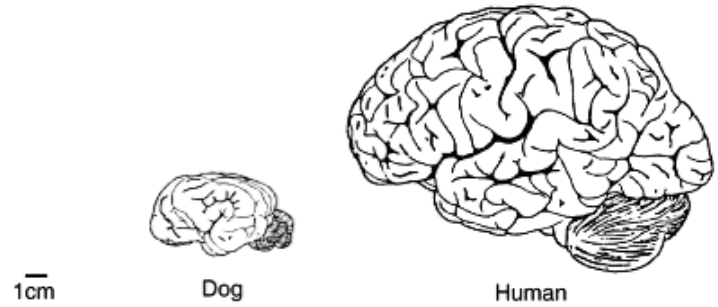

Figure 1 Dog and human brains. Dogs have smaller brains than humans and their cerebral cortex is less folded containing fewer neurons. Adapted from Roth & Dicke (2005) with permission from Elsevier.

The temporal, frontal, parietal and occipital lobes represent a phylogenetically newer portion of the cerebral cortex known as the neocortex (Etsuro 2016). The neocortex is the largest part of human cerebral cortex that takes up about 80 % of the total brain mass (Kaas 2013), but in dogs, the neocortex constitutes a relatively much smaller part of the brain (Jensen 2007). The neocortex integrates sensory stimuli and is responsible for reflection and conscious reasoning. Part of the neocortex is the prefrontal cortex, which constitutes 29% of the total cerebral cortex in the adult human and 12.5% in the dog and it is exceptionally well connected with other brain structures (Brodmann 1909). The prefrontal cortex is generally considered to be the origin of higher cognitive functions, and in primates, it is bigger in size than in other mammals in relative to the rest of the cortex (Preuss 1995; Bush and Allman 2004).

There are five primary cortical areas that receive sensory signals from the brainstem and spinal cord: somatosensory, motor, visual, auditory, and olfactory. The cerebral cortex is mapped according to these functional characteristics. The primary cortical areas provide awareness of sensation, but the recognition of such sensation requires the association of one primary stimulus into more complex sensory combinations (Etsuro 2016).

The limbic system is part of the cerebral cortex and it is common to all mammals and reptiles (Alcock 2009). The limbic system contains the hippocampus, olfactory cortex, parts of the thalamus and the hypothalamus of

the diencephalon. It controls basic behaviors, related to *e.g.* feeding and aggression, connects to sensory areas in the neocortex and is also responsible for attaching emotions to behaviors. The structure and relative size of the limbic system is similar in humans and dogs (Jensen 2007). Based on this similarity, dogs may perceive more or less the same range of basic emotions as humans, but they have a limited capability to reflect consciously on these emotions (Jensen 2007).

Large variations in skull formation and size exist between dog breeds: dog skull length ranges from 7 to 28 cm (McGreevy et al. 2004). This variation is also associated with differences in brain organization in brachycephalic dogs with short noses when compared to dolichocephalic dog breeds with longer noses (Roberts et al. 2010).

This difference can be further associated with differences in behavior, for example increased attention and ability to read human gestures and also differences in trainability and cognitive performance (Helton 2009; Gácsi et al. 2009a). Dog breeds with larger brains perform better on cognitive measures of short-term memory (*e.g.* the ability to remember, after a short delay, under which of multiple containers a treat is hidden) and self-control (ability to inhibit a desire to consume visible food) (Horschler et al. 2019). In humans, variation in skull formation and size is relatively minor, mostly related to sex-specific brain differences (Cosgrove et al. 2007).

It is not known in detail to what extent brain structures in dogs anatomically and functionally correspond to those in humans, and whether those structures underpin similar cognitive functions between species (for a review, Bunford et al. 2017). Recent evidence from fMRI studies support certain correlation between humans and dogs brain structures. Similarities have been found in neural mechanisms of human and dog face processing (Dilks et al. 2015; Cuaya et al. 2016; Thompkins et al. 2018), vocal processing (Andics et al. 2014, 2016), human emotional expressions (Hernández-Pérez et al. 2018) and reward processing (Berns et al. 2012, 2013).

2.3 VISION IN DOGS

Vision is considered to be one of the most important senses in humans, whereas dogs are believed to rely heavily on their excellent olfactory abilities at least in their communication with other dogs (Sjaastad et al. 2010). Relatively little is known about dogs' visual abilities when compared directly with those of humans (for a review, Byosiere et al. 2018). However, the neural circuitry underlying vision is similar in humans and other mammals (Masland and Martin 2007).

The visual perception begins within the retina of the eye. The retina is the innermost layer of tissue of the eye, that is full of photoreceptor cells, rods and cones, that detect light and send impulses via the optic nerve to the visual cortex where information is interpreted as an image.

Dogs' retinas are mostly composed of rod photoreceptor cells (97%), that function in dim light, and provide black and white vision, only 3% of photoreceptors are cone cells, which are responsible for color vision (Peichl 1991; for a review, Byosiere et al. 2018). The area centralis within the retina of humans consists exclusively of cones, whereas in dogs only a minority of the photoreceptors in this area are cones (Movat et al. 2008). Humans' trichromatic color vision is based on three types of cone cells, which are sensitive to all wavelengths (*i.e.* color) of light. Dogs have dichromatic color vision that is based on two types of cone cells, and it has been concluded, that dogs are not able to distinguish green, yellow, and red colors from one other (Miller and Murphy 1995; Neitz et al. 1989; Siniscalchi et al. 2017). However, study results determining which colors dogs can discriminate, have been controversial (Miller and Murphy 1995): to date, at least one study suggested that dogs distinguish blue, red and green from gray color (Tanaka et al. 2000b). In addition to color vision, the canine ability to distinguish brightness affects the dog visual perception. Dogs' ability to discriminate differences in brightness have been estimated to be half that of humans (Pretterer et al. 2004), thus it has been suggested that dogs rely more on color cues than brightness when choosing between visual stimuli (Kasparson et al. 2013).

Dogs' visual system functions well in all lighting conditions, but it is especially adapted to dim light conditions and following movement, probably because their ancestor the wolf needed to locate the potential prey animal (Miller and Murphy 1995). The *tapetum lucidum*, a reflective layer of tissue behind the retina, increases dogs' sensitivity in dim light by reflecting light through the retina a second time (Ollivier et al. 2004). Little research has been done on dogs' motion-detecting abilities, but it has been suggested that dogs can discriminate moving objects at a distance of 800 - 900 m, but the same stationary objects only at a distance of 500 - 600 m (Walls 1963). Dogs can discriminate flickering of light at higher rates than humans (Coile et al. 1989), which could affect their ability to observe images or videos from computer screens. Flicker fusion frequency is observed to be 80 Hz in dogs and 60 Hz in humans (Coile et al. 1989; Healy et al. 2013).

Dogs' sensitivity to light comes at the expense of visual acuity (sharpness or clarity of vision), and their visual acuity is considered to be worse than humans. The number of cones connected to a single ganglion cell determine the visual acuity. Primates have the highest visual acuity (one-to-one cone-ganglion cell ratio), and in cats and probably also dogs the ratio is 1 to 4 (Miller and Murphy 1995). Estimates of dogs' visual acuity have varied greatly owing to difference in research methods, which include behavioral tests, measuring visually evoked cortical potentials or pattern electroretinography (Tanaka et al. 2000a; Odom 1983). Visual acuity has been estimated to be three times higher in humans than in dogs in both bright and dim light conditions (Lind et al. 2017). It has been estimated, that dogs' visual acuity is 6/18 to 6/26, which means that a dog can see clearly a stationary object placed 6 meters away, whereas a person with normal vision can see it from 18 - 26 meters way (Miller and Murphy 1995; Tanaka et al. 2000a).

There are anatomical differences between human and canine eyes, which has an effect on the visual sensation. In humans, the area of sharp central vision (fovea) is located in the *macula lutea*, near the center of retina. The best visual acuity, foveal vision, is only within a visual angle of 1 - 2°, and for the peripheral areas within the visual field and outside the focus of the gaze, the visual acuity decreases dramatically (Yang et al. 2002). Wolves and dogs do

not have a fovea, but instead they have a horizontal visual streak, which is the area of best visual acuity (Peichl 1992).

Visual processing occurs mainly in occipital cortex in humans (Reichert 1992), in dogs (Willis et al. 2001; Sjaastad et al. 2010), cats (Hubel and Wiesel 1959; De Lahunta 1983) and non-human primates (Hubel et al. 1978). The primate cerebral cortex contains over 30 regions implicated in visual processing, which occupy the occipital lobe and parts of the temporal cortex. Temporal cortex regions include areas which contain neurons responsive to faces (Van Essen 1979; Perrett et al. 1982; Felleman and Van 1991; Dilks et al. 2015).

The brain areas involved in visual processing are not fully explored in dogs, but it has been found that cats have 13 visual processing regions in cerebral cortex, so it can be assumed that dogs also have several visual processing areas (Tusa and Palmer 1980; Sjaastad et al. 2010). In mammals, the optic nerve axons from the retinal ganglion cells in each eye meet at the optic chiasm, where the fibers cross and the visual information of the left visual field is processed by the right hemisphere and vice versa (King 1987). Through the optic tract visual information is further sent to the lateral geniculate nucleus (LGN) in the thalamus and to the primary visual cortex (V1), which is located in the occipital lobe (Van Essen 1979, Figure 2). V1 is the earliest cortical visual area processing of all visual information necessary for perception. Neurons in the V1 area are sensitive to particular visual stimuli, such as vertical or horizontal boundaries, color, moving objects and size of stimuli. After V1, information is sent for further processing onto the visual association cortex, which is located within the posterior parietal lobe and posterior temporal lobes. In addition, this information is also passed to different areas of the extrastriate visual cortex including all of the occipital lobe areas surrounding the V1 area (Van Essen 1979; Uemura 2015).

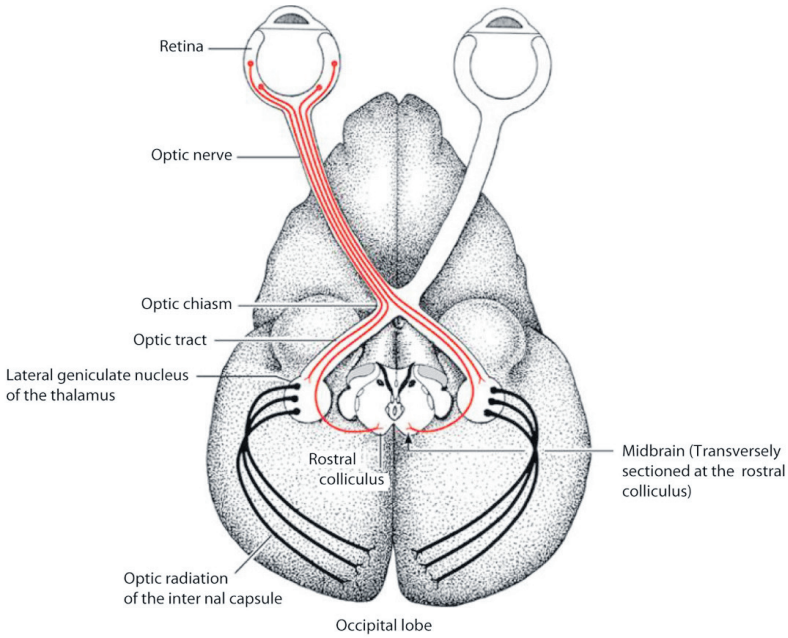

Figure 2 Ventral view of the dog's brain. Visual information is sent from retinal ganglion cells of the eyes through the optic nerve to the optic chiasm, where optic nerve fibers cross. Optic nerve fibers end in three nuclei: 1) the lateral geniculate nucleus of the thalamus, which sends information to the visual cortex located in occipital lobe, 2) the rostral colliculus that is center for visual reflexes, and 3) the pretectal nucleus responsible for constriction of the pupils. Adapted from Uemura (2015b) with permission from Blackwell Publishing.

Dog breeds vary in their head shapes and eye positions, which may result in differences in visual processing (Hart et al. 1995; Wayne and Ostrander 2007). McGreevy et al. (2004) found that, in dolichocephalic dogs with long noses retinal ganglion cells were concentrated in a horizontal visual streak across the retina, but in brachycephalic dogs with short noses those cells were concentrated in an area centralis with no visual streak. The horizontal orientation of the visual streak is thought to be beneficial for hunting (Miklósi 2014): a wider visual streak possibly enhances the ability to detect stimuli across a wider field of view at the cost of discriminating fine details (for a review, Byosiere et al. 2018). In general, dogs' visual field is wider than in humans (240° – 290° versus 180°), which gives dogs a greater ability to scan the horizon. However, binocular overlap (scene viewed by both eyes) is greater in humans than in dogs (140° versus 30 – 60°) (Miller and Murphy 1995). Eye position in brachycephalic breeds is more lateral than in

dolichocephalic breeds resulting in more binocular overlap because the muzzle is not obstructing the field of view (Evans and De Lahunta 2013).

Morphological characteristics affecting the dog's vision might also be associated with performance in cognition tasks. In a commonly used object-choice task, a human experimenter kneels or stands between two containers, one of which contains a food bait, and waits until the dog makes eye contact. The experimenter then gestures towards one of the containers. If the dog chooses the baited container, it serves as reinforcement for a correct choice. Larger dogs have been found to perform better on an object-choice task than smaller dogs, probably because larger dogs have a greater inter-ocular distance, which may improve the use of depth cues (Helton and Helton 2010). Also dogs with short muzzles and forward-facing eyes are more successful in an object-choice task than dogs with long muzzles which is explained by short muzzled dogs more focused visual attention on the human signaler (Gácsi et al. 2009b). However, a meta-analysis of object-choice tasks did not find any differences between dog breed groups (Dorey et al. 2009). Nevertheless, visual capacities can also differ between dog breeds that are bred for different purposes (Peichl 1992). Visual acuity might be better for example in dogs that hunt by their sight (*e.g.* greyhounds) than with their scent (*e.g.* basset hounds). In addition, the developmental environment can influence a dog's later perceptual abilities, since the stimulation from the environment can affect survival of the neurons in the brain or in a sensory organ (Hubel and Wiesel 1998; Miklòsi 2014).

Many of the cognitive research tasks used in dogs are adapted from human or monkey studies and are based on vision. These kinds of tasks include for example the extensively used pointing tasks, where a dog locates food by following human hand direction (*e.g.* Soproni et al. 2002), face recognition tasks (*e.g*. Adachi et al. 2007; Somppi et al. 2014) and studies, that use touch-screen for testing visual discrimination (*e.g.* Range et al. 2008). Dogs' visual discriminatory abilities have been tested using two-choice discrimination paradigms, where dogs are trained to discriminate between two objects or stimulus images. Dogs are rewarded with food in the training phase from their

positive choices (*e.g.* touching the correct image with their nose) or not rewarded from negative choices (*e.g.* touching the incorrect image).

Dogs have been taught to discriminate horizontal and vertical gratings (Lind et al. 2017), different objects (Milgram et al. 1994), objects of different sizes (Tapp et al. 2004; Byosiere et al. 2017) and different quantities (Baker et al. 2012; Petrazzini and Wynne 2016). In a recent study, dogs were more successful at discriminating larger size than smaller size stimuli, which suggests that dogs have difficulties in discriminating fine details of the stimuli (Byosiere et al. 2017; for a review, Byosiere et al. 2018). At the time the work of this thesis began, research into dogs' ability to differentiate objects from each other had just started. But during the thesis dogs were found to be capable of many kinds of categorization, which had been studied in visual and auditory experiments (*e.g.* Adachi et al. 2007; Range et al. 2008; Racca et al. 2010; Autier-Dérian et al. 2013; Somppi et al. 2014, 2016, 2017; Albuquerque et al. 2016; Barber et al. 2016).

2.4 SOCIAL COGNITION IN DOGS

Apart from wolves, dogs have a strong tendency to use their gaze to communicate with humans and they also alternate glances to a human more frequently than wolves when given a problem-solving task that is unsolvable (Miklósi et al. 2003; Kubinyi et al. 2007). Furthermore, dogs' social-cognitive abilities seem more flexible than those of our nearest primate relatives, such as chimpanzees, bonobos, and other great apes (Hare and Tomasello 2005; for a review, Miklósi and Soproni 2006). Compared to dogs, all primates are poor at finding hidden food using social-communicative cues provided by a human (*e.g.* Anderson et al. 1995; Call et al. 2000). However, primates outperform dogs when physical cues are used such as food making a noise when container is shaken (Bräuer et al. 2006). The lack of utilizing social-communicative cues given by a human may be related to competitiveness; primates hardly ever in their natural environment experience a situation in

which one individual cooperatively indicates to another individual the location of food (for a review, Miklósi and Soproni 2006).

Different theories have been proposed to explain how dogs have acquired responsiveness to human social cues (for a review, Reid 2009). One proposal is that during domestication, dogs were selected for their social-cognitive abilities, which enabled them to communicate with humans in unique ways (Hare et al. 2002; Hare 2007). A second assertion assumes that in their interactions with humans, dogs learn through conditioning processes to be responsive to human social cues (for a review, Udell and Wynne 2008). According to a third explanation, co-evolution with humans have equipped dogs with cognitive skills to understand our mental states (Polgárdi et al. 2000; Miklósi et al. 2004). Lastly it has been proposed that dogs are predisposed to learn human communicative gestures (for a review, Reid 2009).

Underlying human social interaction is the Theory of Mind (ToM): the ability to think about our own and other's mental states, such as thoughts, beliefs, and emotions (for a review, Carlson et al. 2013). At present, there is no scientific consensus or enough empirical evidence about whether, or to what extent, non-human animals understand other individuals' minds (Premack and Woodruff 1978; Hare et al. 2001; Penn and Povinelli 2007). Based on dogs' social cognitive skills, it has been suggested that dogs may possess at least a precursory theory of mind or an ability to take others perspective (*e.g*. Miklósi et al 2004; Gácsi et al. 2004; Bräuer et al. 2004). Dogs are sensitive to the attentional states of people: dogs take the 'forbidden' piece of food more often if the experimenter's back is turned, their eyes are closed, or they are engaged in a distracting activity. This contrasts with the scenario when the experimenter is looking at them (Call et al. 2003). Dogs are also less likely to beg from a person facing away from them or wearing a blindfold (Gácsi et al. 2004). However, these performances do not require ToM. They only require that dogs have learned through past experiences, the cues associated with reward and non-reward, such as people are unlikely to give them food without paying attention to them (for a review, Emery 2000; Udell and Wynne 2008).

In humans, the ability to recognize faces based on visual cues is an important part of social cognition (Bruce and Young 1998). The face provides

information about individual's identity, age, gender, familiarity, emotional and mental states. Faces are differentiated and recognized with superior efficiency compared with objects, and face-sensitive neural mechanisms are involved in facial processing (*e.g.* Farah 1996; McKone et al. 2007). Multiple studies have also demonstrated that dogs are able to discriminate faces based on visual or audiovisual cues. Dogs can differentiate between canine and landscape images (Range et al. 2008), canine and human faces (*e.g.* Racca et al. 2010), familiar and unfamiliar faces (Nagasawa et al. 2011; Somppi et al. 2014; Eatherington et al. 2020), canine and non-canine faces (Autier-Dérian et al. 2013) and emotional expressions (Nagasawa et al. 2011; Müller et al. 2015; Somppi et al. 2016). In addition, dogs can integrate bimodal sensory information. In an auditory experiment, dogs were presented with a picture of their owner's face or the face of a stranger and the voice of one of those. Dogs looked at the owner's picture longer when the picture did not match the voice suggesting that the dogs generated a visual image from the auditory information (Adachi et al. 2007). A similar study showed that dogs looked longer at the human or canine face whose expression was congruent to the emotional valence of vocalization (Albuquerque et al. 2016). Besides dogs, the ability to discriminate conspecifics from visual cues have been demonstrated in many other species, *e.g*. in sheep (Kendrick et al. 1995), in cattle (Coulon et al. 2011) and in monkeys (Fujita 1987; Pascalis and Bachevalier 1998).

2.5 DOG COGNITION RESEARCH METHODS

2.5.1 BEHAVIORAL STUDIES

Dog cognition has been extensively studied with different kinds of behavioral experiments, and the tests have been used as an indicator of cognitive differences between dogs and wolves (Miklósi et al. 2003; Kubinyi et al. 2007; see review, Bensky et al. 2013). Dogs have been shown to be more skilful than great apes and wolves in an object-choice task following basic human

pointing cues to locate food and also to generalize this behavior to relatively novel human movements such as pointing with leg (*e.g.* Hare and Tomasello 1999; Soproni et al. 2002). These findings suggest that during domestication, dogs evolved specialized skills to read human social and communicative behavior (Hare et al. 2002; Hare and Tomasello 2005).

Problem solving tasks, especially object manipulation, have been widely utilized when comparing dog and wolf intelligence (*e.g.* Frank and Frank 1985; Hiestand 2011). One of the object manipulation tasks is a means-end task that has been used to study dogs' understanding of how a combination of actions leads to a goal, *e.g.* by pulling a string the dog obtains access to a piece of food (Osthaus et al. 2005; Range et al. 2011). In means-end tasks, the problem solver has to first envision the goal, and then decide the best actions for achieving the goal in the current situation. Evaluation of means-end understanding is an important area of comparative cognition; it can be considered a key mental prerequisite of higher cognitive abilities such as tool use (Helme et al. 2006; Schuck-Paim et al. 2009). Second, the object manipulation tasks have been used to compare independent problem-solving skills between dogs and wolves. In tasks such as manipulating a box to gain access to a food dish, more persistent and independent wolves performed better than dogs that give up sooner and seek help from human experimenter (Frank 1980; Frank and Frank 1985).

Looking-time experimental paradigms, relying on the assumption that dogs direct their attention to interesting targets, are adapted from pre-verbal infant studies (Berlyne 1958; Fantz 1958). Typically, two pictures are presented side-by-side and the dog's attention to a certain image or object is evaluated from video recordings (*e.g.* Adachi et al. 2007; Racca et al. 2010). However, video recording techniques relying only on the direction of the dog's head lack spatial accuracy and they allow only gross judgements of the direction of the dog's gaze (Williams et al. 2011). Besides the behavioral tests, other methods are also necessary to obtain information about the cognitive and neural processes underlying a dog's behavior.

2.5.2 MEASURING BRAIN FUNCTION

Electroencephalography (EEG) is a brain imaging technique that measures electrical activity generated by neuronal cells (Berger 1929). In humans, EEG is standardly measured completely non-invasively from the surface of the head with electrodes that are placed on the scalp in specific positions. This technique uses the international 10/20 system to maintain the relative distances between electrodes constant (Jasper 1958). In dogs, no standardized system exists for EEG measurements, thus different kinds of electrodes and different positioning have been used in canine studies. The electrical activity is generated by synchronously active groups of neurons in the cerebral cortex, oriented in the same direction. Large populations of simultaneously active neurons are needed in order to record their electrical activity on the head surface, because the current needs to penetrate the skull, muscles, and skin. The recordable neural activity is the summation of the excitatory and inhibitory postsynaptic potentials of synchronously firing pyramidal neurons. EEG records voltage differences between two electrodes: active and reference electrodes (Caton 1875; Berger et al. 1929; Teplan 2002; Britton et al. 2016).

EEG is a powerful tool in neurology and clinical neurophysiology due to its ability to reflect normal and abnormal electrical activity of the brain in millisecond-scale temporal resolution (Niedermeyer and da Silva 2005). In dogs, EEG has been mostly used as a diagnostic method in epilepsy research (Berendt et al. 1999; Jeserevics et al. 2007; Jokinen et al. 2007; James et al. 2011; De Risio et al. 2015; James et al. 2017). Although scalp-EEG is widely utilized in humans, there are only a few recent studies where fully non-invasive EEG method has been used in unsedated dogs (Kujala et al. 2013; Kis et al. 2014; Kis et al. 2017a; Bunford et al. 2018), all of which are either concurrent with or subsequent to the data of this thesis. In addition, Howell et al. (2011, 2012) used minimally-invasive EEG with needle electrodes to study mismatch negativity potential related to novel auditory stimuli. In general, previous EEG studies in animals have mainly been invasive, and therefore animals need to be sedated or anesthetized, which limits the subject of the study and can

influence cognitive processing (Koelsch et al. 2006). Kis et al. (2014, 2017a) studied canine sleep with the non-invasive polysomnography method (see also Bunford et al. 2018). Sleep studies might be easier to perform than conscious recordings in moving dogs, but they make it impossible to study the vast majority of cognitive processes, for example visual and attentional processes. For this purpose, the event-related potential (ERP) technique is more suitable.

In humans, many ERP components are well recognized and characterized (Otten and Rugg 2005), but in non-human species they have been studied less frequently owing to differences in research traditions. The advantages of measuring ERPs are that they reflect ongoing neural activity with almost no delay, and that they can be measured noninvasively from any group of participants (*e.g.* infants and dogs) without any behavioral response (Luck 2012). However, ERP measurements have relatively low spatial resolution compared for example with the functional magnetic resonance imaging (fMRI) technique.

Contrary to EEG, fMRI can provide millimeter-scale information about the area in which brain information is processed, but with much lower temporal precision, time lag of 300 - 1000 ms (Glover et al. 2011). fMRI detects active brain areas by measuring oxygenation level -dependent changes in blood flow (Huettel et al. 2004; Dalenberg et al. 2018). In humans, fMRI has become the prominent method in cognitive neuroscience studies and during the last decade a highly popular method also in dogs. In dogs, conscious fMRI testing requires them to be trained to stay still and to wear earmuffs during the measurements. fMRI has been used for studying the regions of the dog's brain that are related to human hand signals (Berns et al. 2012, 2013; Cook et al. 2014), face processing (Dilks et al. 2015; Cuaya et al. 2016), human and dog vocalization responses (Andics et al. 2014), analyzing and integrating word meaning and intonation (Andics et al. 2016), olfactory responses (Jia et al. 2014) and cognitive control (Cook et al. 2016).

2.5.3 EYE GAZE TRACKING

Eye tracking is a non-invasive method that can be used to study for example visual, attentional, emotional, and cognitive processes in humans and animals. Compared to visual inspection of head and gaze direction of dogs (*e.g.* Adachi et al. 2007; Racca et al. 2010), eye gaze tracking allows eye movement data collection at finer temporal and spatial resolution (Park et al. 2020). Generally, the eye tracker sends invisible harmless infrared rays into the observer's eyes and tracks the reflection of the rays to obtain information about the observer's eye movements *e.g.* fixations and saccades. Fixations are eye movements that stabilize the eyes to an object of interest, and they can last from 10 of milliseconds up to several seconds in humans. Saccades are rapid eye movements that are used to reorient the eyes from one fixation to another about three times each second (for a review, Rayner 1998; Duchowski 2007). During a saccade no new information is acquired because the eyes are moving so quickly that only blur would be perceived (Uttal and Smith 1968; for a review, Matin 1974).

Utilizing eye gaze tracking, we can follow, almost in real-time, where attention is directed and what the research subject finds interesting. In most eye trackers the sampling frequency is between 25 - 2000 Hz, which refers to how many times per second the position of eyes is measured, for example for a 250 Hz eye-tracker a sample is taken once every 4 ms (Andersson et al. 2010). The interesting or important objects in a scene are often inspected first and attract longer viewing time than less interesting objects (for a review, Rayner 1998; Henderson 2003; Duchowski 2007). In humans, non-intrusive eye tracking is a common research method and it has been used since Buswell (1935). Eye tracking research has revealed much about the cognitive processes underlying human behavior and it is useful in various research fields such as psychology, marketing, and human computer interaction (*e.g.* Yarbus et al. 1967; Gredebäck et al. 2010; Holmqvist et al. 2011).

Eye gaze tracking is a relatively novel method in dogs, and at the beginning of this thesis work there were no scientific publications of eye tracking in dogs. Williams et al. (2011) was the first to develop a head-mounted eye tracking

system for dogs, which allowed eye movement tracking even when the dog was moving (see also preliminary results, Rossi et al. 2014). As the eye tracker is attached to the dog's head, it requires training to ensure the dogs are habituated to the apparatus. Calibration of the eye tracker can also be challenging, because the dog needs to fixate calibration points with minimal head movements in order to accomplish accurate calibration (Williams et al. 2011). Head-mounted systems have been developed also for use in other animal species such as chimpanzees (Kano and Tomonaga 2013), chickens (Schwartz et al. 2013) and rats (Wallace et al. 2013).

Contrary to head-mounted systems, remote eye trackers enable eye gaze tracking without direct contact to the subjects, but they are usually relatively sensitive to subjects' head and other movements. Remote eye tracking has been used in several comparative cognition studies in primates (*e.g.* Dahl et al. 2007, 2009; Hirata et al. 2010; Kano and Tomonaga 2009, 2010; Leonard et al. 2012; Myowa-Yamakoshi et al. 2012; Paukner et al. 2013) and also recent studies in dogs (Téglás et al. 2012; Somppi et al. 2014, 2016, 2017; Barber et al. 2016; Kis et al. 2017b; Gergely et al. 2019), all of which are concurrent with or subsequent to the commencement of this thesis.

3 AIMS OF THE STUDY

The first aim of the experiments in this thesis was to evaluate the feasibility of novel non-invasive electroencephalography (EEG) and remote eye gaze tracking methods in dogs. Second aim was to compare human and dog cognitive abilities by using eye gaze tracking. More detailed research questions were:

1. Can non-invasive EEG be reliably used in dog cognition studies, and can dogs' early visual event-related potentials (ERPs) be measured in human and dog faces (Experiment I)?
2. Can eye gaze tracking be reliably used in dog cognition studies and for comparison of eye movements between humans and dogs? Do dogs focus their attention to the presented images and biologically relevant areas in them (Experiments I–IV)?
3. Do dogs differentiate between images according to their categorical content, and does the composition of the images affect the dogs' gazing behavior (Experiments I–IV)?
4. Do dogs and humans differ in their gazing behavior of images with social and non-social content (Experiment III)?
5. Do two dog populations living in different social environments differ in their gazing behavior (Experiments III and IV)?

4 MATERIALS AND METHODS

4.1 PARTICIPANTS

Four experiments were conducted between years 2010 - 2012 at the University of Helsinki (Table 1). All the experiments were ethically pre-evaluated and accepted by the Viikki Campus Research Ethics Committee before the start of the experiments.

Table 1 Electroencephalography (EEG) was measured in one experiment and eye tracking was used in three experiments.

Exp.	Exp. conducted (year)	Article published (year)	Research method	Exp. focus
I	2011	2013	Electro-encephalography (EEG)	Non-invasive EEG measurement in dogs
II	2010	2012	Eye tracking	Contact-free eye tracking in dogs
III	2012	2015	Eye tracking	Comparison of eye movements between humans and dogs
IV	2011	submitted	Eye tracking	Observation of natural scenes by dogs

4.1.1 FAMILY AND KENNEL DOGS

In total, 84 dogs were included in experiments (Table 2), and some of these dogs were included in multiple experiments. In experiments II - IV 6 – 38 family dogs participated, representing many breeds and sizes. Family dogs were 1 – 10 years old and lived with their owners. Their daily routine consisted of food provision once/ twice a day and being taken outdoors three to five times. In addition, 8 purpose-bred beagles participated in experiments I, III and IV.

During the experiments, the kennel dogs were 4 – 6 years old, and they lived in a kennel-like environment as a social group at the facilities of University Helsinki. Kennel dogs seldom met other dogs or humans except the caretakers and the researchers with whom they were familiar. Kennel dogs were fed two times a day and released into an outside area every day for 2 hours. After the experiments, all kennel dogs were re-homed to private families. All the dogs had normal vision as evaluated by their owners or caretakers.

Table 2 Number, sex and breeds of dogs that participated in the experiments.

	Exp.I	**Exp.II**	**Exp.III**	**Exp.IV**
Family dogs	–	6	38	16
Females	–	5	31	11
Males	–	1	7	5
Kennel dogs (Beagles)	8	–	8	8
Females	2	–	2	2
Males	6	–	6	6
Total number of dogs	8	6	46	24
Australian kelpie	–	–	1	–
Beauceron	–	3	3	3
Border collie	–	–	7	1
Boxer	–	–	2	–
Bouvier des Flandres	–	–	1	–
German pinscher	–	–	1	–
German shepherd	–	–	3	–
Great Pyrenees	–	1	1	1
Hovawart	–	1	3	2
Lagotto Romagnolo	–	–	1	1
Manchester terrier	–	–	1	–
Miniature poodle	–	–	2	–
Miniature schnauzer	–	–	1	–
Mixed breed	–	–	3	2
Rottweiler	–	–	1	–
Rough collie	–	1	2	2
Smooth collie	–	–	1	2
Swedish shepherd	–	–	1	1
Welsh corgi cardigan	–	–	3	1

4.1.2 HUMANS

In experiment III, human data from 26 volunteers were included: a completely re-analysed subsample from a previous experiment (Kujala et al. 2012). There were two groups of humans: dog experts and non-experts. Dog experts (9 females, 4 males, age 31.9 ± 6.6 years) owned a dog/dogs and had extensive experience of dogs. Non-experts (5 females, 8 males, age 28.2 ± 7.5 years) did not own a dog and they had little experience of dogs. All the participants had normal vision or corrected-to-normal vision.

4.2 STIMULI

In experiments I – IV, the stimuli were specifically chosen to be able to study cognitive and neural processes related to image categorization and viewing natural social scenes (see Figure 3 for examples). For experiments I, II and IV, images were obtained from personal collections and image databases on the internet (*e.g.* 123RF and bigstockphoto). In experiment III, a selection of 60/200 original images from a previous human study (Kujala et al. 2012) were chosen for the comparative study between dogs and humans.

The stimuli in experiments I–II were close-up images of faces, objects, and characters, detached from their original backgrounds. In experiment I, the stimuli consisted of color images of 36 upright human and 39 dog faces, and 3 inverted human and 3 dog faces (Figure 3). Inverted faces were part of another experiment with different aim, and their small total number of stimuli did not result in an adequate signal-to-noise ratio to allow comparisons with the other image categories. However, inverted images were used for the general feasibility analysis of the brain responses. The facial images were approximately 550 x 600 pixels (px) in size. All the faces were detached from their original background and placed on a gray background. In experiment II, color images of 29 human faces, 27 dog faces, 12 children's toys and 15 alphabetic characters were used as stimuli. The images were presented on a gray background and were 750 x 536 px in size.

In experiment III, the stimuli consisted of natural full-body images of dogs and humans within a neutral background, and artificially created control

images. More specifically, the stimulus images were color photos of two dogs facing towards each other and greeting by sniffing or playing; two dogs facing away from one another; two humans facing each other and greeting; and two humans facing away from one another. In addition, in experiment III crystallized pixel images were used as control stimuli, taken from a random sample of both interactive and non-interactive image conditions. There were 12 images per category. The dog images were 567 × 397 px and the human images 640 × 480 px placed on a grey background. Images were of equal physical dimensions (20 x 14 cm) in human and dog studies.

The stimuli in experiment IV were natural full-body color images of dogs, humans, and wild animals (*e.g.* elephants, tigers, pandas), either close-up or within their natural surroundings (Figure 3). There were three categories of images: 1) landscape images that contained a human or an animal, 2) single human or animal full body images 3) full body images of two paired humans or animals (4 human and 4 animal images per each category). Images were 725 x 550 px in size overlaid on a grey background.

Figure 3 Two images from the left: Examples of dog and human face images used in Experiment I. Two images from the right: Example images from experiment IV (full-body image of paired wild animals and landscape image containing a dog).

For dogs, stimuli were presented with Presentation® software (Neurobehavioral Systems, San Francisco, CA, USA) in experiments I and II. In experiments III and IV, stimuli were shown using Experiment center™ 3.0 software (SensoMotoric Instruments GmbH, Berlin, Germany). The images were delivered on a 22-inch (47.4 × 29.7 cm) liquid-crystal display (LCD) monitor. For humans in experiment III, the stimuli were shown with Presentation® software (Neurobehavioral Systems, San Francisco, CA, USA)

and shown on a projection screen by a data projector (Christie Vista x3, Christie Digital Systems Inc., Cypress, CA, USA).

4.3 TRAINING OF THE DOGS

Before the experiments, dogs were trained to lie still and lean their head on a chin rest, because dog's movements cause severe artifacts in the EEG and eye tracking data. Kennel dogs were also accustomed to wearing a custom-made vest with a pocket, which held the lightweight EEG amplifier was (Figure 4). Dogs were trained with a positive operant conditioning method (clicker) to lie 1 minute on a 10 cm tick Styrofoam mattress and lean their head on a purpose-designed u-shaped chin rest. Dogs were not trained to fixate on the monitor or images. To pass the training period, a dog had to take the pre-trained position on their own (without any command from the trainer) and to remain in that position for at least 30 seconds while the owner/ experimenter was behind an opaque barrier.

Family dogs were trained during 1 – 2 months before the experiments by their owners as instructed by the experimenter. Dogs also visited the experiment room with their owners, 2 – 9 times to become accustomed to the room and setup. Kennel dogs were trained during an 18-month period by the experimenters. Kennel dog training took longer than that of the family dogs, because they were less used to the training situation and had less obedience training experience previously than the family dogs. Kennel dogs were also trained for the task less often than family dogs.

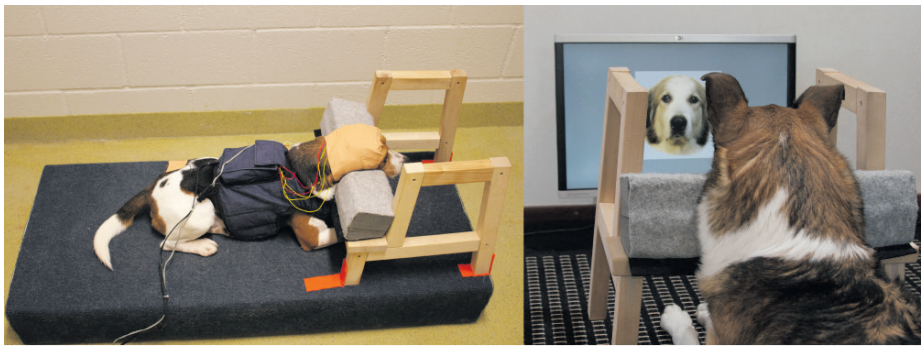

Figure 4 Left: The experimental setup during the EEG measurement. The dogs were lying on a mattress and leaning their head on a chin rest while observing the stimuli from the computer monitor. The dogs were also carrying the dog vest with the EEG amplifier. Right: A dog watching images from computer monitor during eye tracking. The eye tracker was mounted under the monitor (eye tracker not visible in picture). The experimental setup was similar to the EEG setup except the dogs were not wearing the EEG equipment.

4.4 ELECTROENCEPHALOGRAPHY

4.4.1 OVERVIEW

EEG is a widely used method for investigation of brain function and for determining the reactions of the brain to particular stimuli. Event-related potentials (ERPs) are electrical potentials produced by the brain in response to specific internal or external events (Storm van Leeuwen et al. 1975; Callaway 1978). For a visual stimulus, the first major ERP component is the P1 wave with a peak latency of approximately 100 ms. The P1 is followed by the N1 wave peaking around 100-200 ms after stimulus onset, which has been identified non-invasively from humans (*e.g.* Hillyard and Münte 1984; O'Donnell et al. 1997) and intracranially in monkeys (*e.g.* Pineda et al. 1994; Woodman et al. 2007) and in dogs (*e.g.* Bichsel et al. 1988; Lopes da Silva et al. 1970 a, b). N1 has several subcomponents (Fabiani et al. 2007; Luck 2012). The widely studied N170 wave is associated with the processing of faces: the amplitude of N170 is stronger when facial stimuli are presented compared to non-facial objects (Puce et al. 1995; Kanwisher et al. 1997; for a review, Haxby et al. 2000). ERPs are not recognized from raw EEG data, so they are extracted by digital averaging of recording periods of EEG time-locked to

different events (Dawson 1954; Teplan 2002; Luck 2012). Prior to this thesis, there were no non-invasive ERP studies in dogs, and only one ERP study where a dog's reactions to auditory stimuli was measured with one needle electrode (Howell et al. 2012), therefore we wanted to explore the usability of non-invasive ERP technique in dog cognition studies.

4.4.2 MEASUREMENT

Experiment I included EEG measurements from eight dogs. The EEG was measured with an ambulatory Embla® Titanium™-recorder, RemLogic ™ 2.0 -software (Embla Systems) and custom-made trigger system. The size of the EEG recorder was 3.5 x 7.5 x 11.4 cm and it weighted 200 g. Disposable Unilect™ (Unomedical a/s, Birkerod, Denmark) neonatal electrodes with bioadhesive gel and cloth were used in the measurements. The hair on top of the dog's head was shaved, NuPrep™gel (Weaver and Company, Aurora, CO) was rubbed on the skin and the skin was cleaned with isopropyl alcohol. To keep the electrodes in place, drops of cyanoacrylate glue were applied to the corners of the electrode pads before the electrodes were attached to the skin. Additionally, medical elastic tape was attached to the top of the electrodes. The EEG was measured with seven electrodes: Fp1 and Fp2 above the eyes, F3 and F4 located cornerwise from the previous in the postero-lateral direction, Cz in the middle, and P3 and P4 on the back of the dog's head (Figure 5). Before the EEG measurements, the locations of the electrodes were visualized with respect to each dog's brain using computed tomography (CT) images acquired with a Somatom Emotion Duo scanner (Siemens Medical Solutions, Erlangen, Germany). The locations of the electrodes were displayed with calcium pills placed on the surface of the dog's head. The y-linked reference electrodes were placed on the dog's ears, and the ground electrode was attached at the lower back. The impedances of the electrodes were checked three times during each measurement to be sufficient, and the EEG signals were band-pass filtered to 0.15–220 Hz and digitized at 512 Hz.

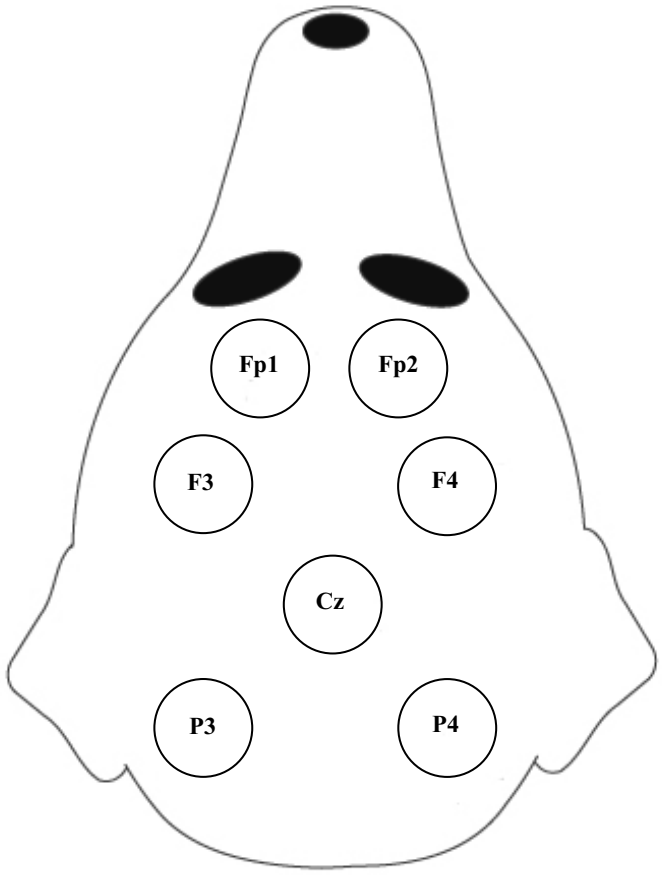

Figure 5 The layout of the electrodes on the dog's head.

4.4.3 ANALYSIS

The EEG data analyses were conducted with Matlab R2010B (Mathworks Inc, Massachusetts, USA). All trials, where dog movement was detected, or EEG channels' amplitude exceeded 200 μV, were discarded from further analyses to prevent data contamination by external artifacts. Each dogs' EEG traces were averaged across single trials from –200 ms prior to 400 ms after stimulus onset, and 30 Hz low-pass filtering was used. To statistically confirm individual level ERPs, a standard deviation was determined from the baseline period of

-200 ms to 0 ms separately in each EEG channel, and the statistical threshold level was set to 3.291 standard deviations, which corresponds to the significance level of $p < 0.001$ of the estimated t statistics. After that, all the time points from 0 to 400 ms were statistically tested against the baseline level, to reveal significantly differing brain responses from the baseline level. For the group analysis, the response of individual dogs was normalized with respect to the maximum modulation during the 0 – 400 ms time period (with respect to the –200 to 0 ms baseline period), so that the maximum amplitude was given value 1 and the rest of the responses were scaled accordingly. This made it possible to scale the responses of all dogs similarly and to ensure that any single dog's responses did not drive the group-level effect. After that, a group-level grand average of eight dogs was made by averaging together the individual traces, and the group-level responses from 0 to 400 ms were compared to zero (one-sample t tests, $p < 0.001$). For species-related testing, group level grand averages of ERP traces were calculated for the human and dog face categories separately, and the responses to the human and dog faces were compared using paired-samples t tests ($p < 0.01$).

4.5 EYE TRACKING

4.5.1 OVERVIEW

By eye tracking we can obtain some insight into what the observer found interesting and what drew his/ her attention for example towards a certain point in an image. Eye tracking is a widely applied method in studies of cognitive processes in humans (Duchowski 2017), and recently also in non-human primates (*e.g.* Dahl et al. 2007; Kano and Tomonaga 2009) and in dogs (*e.g.* Téglás et al. 2012; Somppi et al. 2014).

Given that eye tracking is a relatively new technique to be used in dogs, there is a lack of information regarding the length and speed of dogs' fixations and saccades. In the eye tracking analyses of this thesis, based on a study conducted in monkeys (Kano and Tomonaga 2009), a fixation was coded if the minimum fixation duration was 75 ms, and the maximum dispersion value

D = 250 px {D = [max(x) − min(x)] + [max(y) − min(y)]}. Elsewise the recorded data sample was defined to be part of the saccade. A low-speed event detection algorithm was used for scoring the fixations. It calculates potential fixations with a moving window spanning consecutive data points.

Before an eye tracking episode, the eye tracker must be calibrated to each participant's eyes in order to collect data as accurately as possible. The accuracy of measured eye movements depends on how well the calibration has succeeded. In adult humans, calibration is done by asking the participant to look at certain points on the screen. Based on this, the eye tracker program analyses eye position in each calibration point and calculates coordinates to the gaze direction (Duchowski 2017). In infant or current animal studies, moving targets are commonly used in order to maintain participants attention in these points (Gredebäck et al. 2010; Téglás et al. 2012). Before this thesis project, there were no studies where dogs' eye gaze had been measured with remote eye-tracking. One eye gaze tracking study in dogs was published simultaneously with experiment II of this thesis (Téglás et al. 2012).

4.5.2 MEASUREMENT

Eye tracking was used in Experiments II – IV. Dogs' binocular eye movements were measured at a sampling rate of 250 Hz with an infrared contact-free eye tracker (iView X™ RED250, SensoMotoric Instruments GmbH, Berlin, Germany), based on a corneal reflection (Figure 6). The eye tracker was integrated into an LCD monitor. In experiment II, human monocular eye movements were recorded at a sampling rate of 60 Hz with the SMI MEye Track long-range eye-tracking system (SensoMotoric Instruments GmbH, Berlin, Germany), which is based on video-oculography and dark pupil-corneal reflection.

In dogs (experiments II - IV), the eye tracker was calibrated using a five-point procedure. The screen was replaced with a plywood wall with five 30-mm holes in the calibration point positions, and the experimenter lifted up a flap covering a hole and showed a treat in the hole to catch the dog's attention. Another experimenter accepted the calibration point with the operating

computer program (iView X™, SensoMotoric Instruments GmbH, Berlin, Germany), when the dog had looked at a point for at least 5 seconds. After all calibration points were accepted, the dog was rewarded with a treat. In addition, two calibration check trials were done after the initial calibration. To pass the criterion for an adequate calibration, the dog needed to fixate on the central calibration point and at least three of four distal points within a 1° radius. Calibration and experimental sessions were recorded on separate days in order to maintain the ideal vigilance and to prevent frustration of the dog. The dog and eye tracker position and illumination were kept the same during calibration, calibration check trials and actual experiments. The human eye calibration (experiment III) followed a standard procedure: the calibration was performed by showing five fixation points on the screen, which humans were asked to look at.

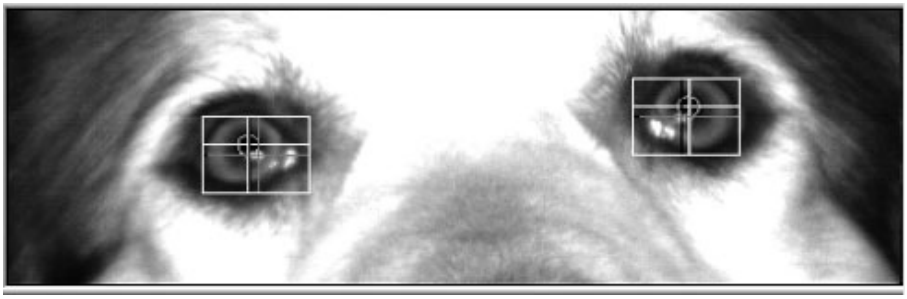

Figure 6 Dogs' binocular eye image from the eye trackers' recording program SMI Experiment center. The eye tracker registers the center of the pupil (white crosshair) and corneal reflection (black crosshair).

4.5.3 ANALYSIS

The eye gaze data were analyzed using BeGaze™ software (SensoMotoric Instruments GmbH, Berlin, Germany). In experiments II – IV, calculations were made from binocular raw data in dogs. In experiment III, gaze parameters were calculated from monocular raw data obtained in humans. Before the statistical analyses, the stimuli were divided into areas of interest (AOI) and gaze variables were calculated for these areas. The statistical analyses were conducted using SPSS statistics (IBM, New York, USA).

In experiment II, repeated linear mixed-effect models were used to analyze the differences in gaze parameters between the familiar and the novel images, between image categories (dog, human, letter, and item), and between the blank screen and image-viewing frames. Each image was divided into three AOI areas: monitor, image, and object. Number of fixations, duration of single fixation, total duration of fixations, and relative fixation duration (the duration of object area fixations divided by the image area fixations) were calculated for each AOI. In the comparison between blank screen and image-viewing frames, the relative fixation duration was the duration of image area fixations divided by the monitor area fixations.

To make the human and dog data comparable in Experiment III, both species' eye movement data were analyzed with a likewise procedure with BeGaze™ software. Repeated-measures analysis of variance (ANOVA) were used to examine the differences between family and kennel dogs, and between human experts and non-experts. *Post-hoc* tests (independent samples t-tests with between-groups and within-groups comparison) were then used to clarify the ANOVA results. Two AOI areas were used: image and object area (the heads and bodies of the two dogs/humans). Pixel images did not have object AOI area. Total gaze time (sum of durations of all fixations and saccades) was calculated for the image area and relative gaze time (the total object area gaze time divided by the image area gaze time) for the object area. Furthermore, the number of saccades between two objects (the transitions of fixations from left object to right object and vice versa) were calculated for the two AOIs.

In experiment IV, the differences between family and kennel dogs' eye movements were studied with repeated-measures analysis of variance (ANOVA), and ANOVA results were clarified with paired samples t-tests. Total gaze times (sum of durations of all fixations and saccades) were calculated for each AOI area (object, background, head, and body). There was variation in the sizes of the AOI areas between image categories and species represented in images, and therefore the gaze time was measured as a normalized score, "proportional gazing time" (applied from Dahl et al. 2009; Guo et al. 2010; Somppi et al. 2016). Calculation of the score was done by subtracting the

relative AOI size (*e.g.* the size of the head divided by the size of the whole object) from the relative gaze time (*e.g.* the total gaze time of the head divided by the total gaze time of the whole object area).

5 RESULTS

5.1 APPLICABILITY OF NON-INVASIVE EEG AND EYE TRACKING IN DOG COGNITION STUDIES

Experiment I explored the feasibility of event-related EEG measurements in dogs and experiments II – IV studied the applicability of eye gaze tracking in studying canine cognitive processes. Experiment I demonstrated the applicability of non-invasive scalp-EEG in studying the neural processes underpinning canine visual cognition and object perception. Early visual ERPs were detected at 75 – 100 ms from the time of the stimulus onset in individual dogs. At the group level, the data of eight dogs at the most posterior sensors (P3 and P4) differed significantly from zero bilaterally at approximately 75 ms. Some variation in the amplitude of the visual N1 response was detected between dogs, even though the latency and the transient form of the responses were similar across individuals.

Experiments II – IV showed that remote eye tracking is a feasible method to study dog cognition related to image viewing. All of the dogs' eyes were successfully calibrated before the experiments, and calibration accuracy was between 84 and 96 %, calculated as a portion of fixated points out five calibration points within a 1° radius in calibration checks from all dogs (Table 3). In Experiment II, six dogs' eye gaze were successfully tracked, and dogs focused their attention on the informative regions of the images: they fixated longer and more often towards the screen when images were shown than when there was only blank screen. The eye gaze tracking succeeded better for one eye than the other. For the better eye, the average tracking ratio (mean percentage of the time pupil was detected during the entire experimental session) was on average 45 %. In Experiment III, successful gaze tracking was gained from 32 family dogs, eight kennel dogs, and 26 humans. Six family dogs were excluded from the analyses due to their restless behavior (*e.g.* leaving repeatedly from the chin rest or turning their heads away from the screen) during the recordings. In experiment IV, eye gaze was successfully recorded from 16 family dogs and eight kennel dogs. Images were excluded

from the analyses due to technical difficulties, eye-tracker software problems or dogs leaving/ lifting their head from the chin rest (Table 3).

Table 3 The calibration accuracy in percentage in eye tracking experiments and number of excluded stimuli from analyses on average per dog or human in all experiments.

Experiment	Research method	Calibration accuracy	Excluded stimuli
I	Electroencephalography	-	74/240
II	Eye tracking	84%	10/143
III	Eye tracking		
	-Dogs	95%	4/60
	-Humans	- [a]	2/60
IV	Eye tracking	96%	5/72

[a] Calibration accuracy was not checked in humans, instead a standard calibration procedure was followed

5.2 CATEGORY-RELATED DIFFERENCES IN DOGS' BRAIN RESPONSES AND GAZING TIMES

All experiments I - IV explored the differentiation of visual categories by dogs. Differences in ERPs between human and dog faces were detected at 75 – 100 ms in the posterior sensors and at 350 – 400 ms in the anterio-temporal sensors in Experiment I. In eye tracking Experiment II, dogs' gazing behavior differed between image categories. All the results in Experiment II were analyzed with repeated linear mixed-effects models. Dogs fixated dog faces more than human faces, items or letters (mean $\pm$ standard error of the mean (SEM), for dog *versus* human 534 $\pm$ 80 ms *versus* 446 $\pm$ 80 ms, $p < 0.05$; for dog *versus* item 534 $\pm$ 80 ms *versus* 294 $\pm$ 80 ms, $p < 0.01$; for dog *versus* letter 534 $\pm$ 80 ms *versus* 94 $\pm$ 120, $p < 0.001$; human *versus* letter 446 $\pm$ 80 ms *versus* 94 $\pm$ 120, $p < 0.01$; letter *versus* item 94 $\pm$ 120 *versus* 294 $\pm$ 80, $p < 0.05$; Figures 7 & 8). Furthermore, dogs fixated on dog images more often (2.0 $\pm$ 0.3) than human (1.6 $\pm$ 0.3, $p < 0.05$), item (1.2 $\pm$ 0.3, $p < 0.01$) or letter images (0.5 $\pm$ 0.5, $p < 0.01$). Statistically significant difference was found in a main effect of the image category on the relative fixation duration of the object

(p = 0.042), but in the pairwise comparisons image categories did not differ from each other (duration of object area fixations divided by image area fixations in percentage: dog 65.4 ± 6.4%; human 56.2 ± 6.7%; item 60.4 ± 8.4%; and letter 39.8 ± 13.3%). In addition, dogs fixated familiar images longer than novel images in all image categories. The first image of the series gathered more fixations (1.8 ± 0.3) than familiar (1.3 ± 0.3, $p < 0.01$) or novel images (0.1 ± 0.3, $p < 0.001$). After the first image the number of fixations decreased ($p < 0.05$) and the duration of single fixation increased ($p < 0.01$). Experiment II also showed that dogs fixated more (2.3 ± 0.4 *versus* 1.1 ± 0.5, $p < 0.001$) and the durations of single fixations were longer (205 ms, 95% confidence interval (CI) 137 – 307 *versus* 128 ms, 95 % CI 85 – 193) at the monitor when images were displayed than when the monitor was blank.

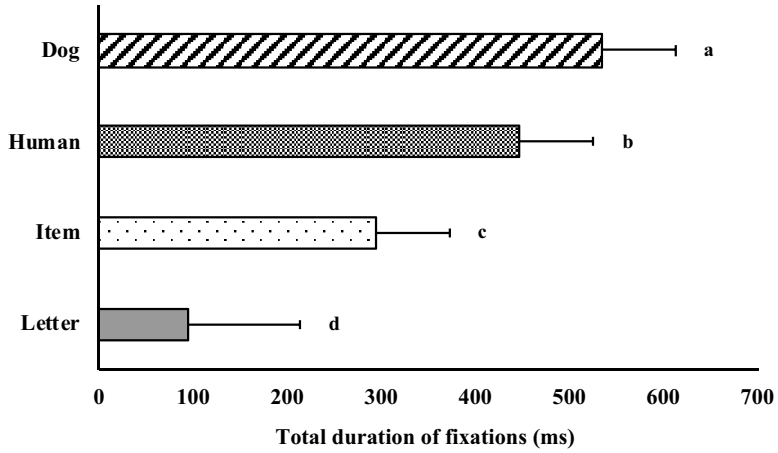

Figure 7 Total duration of fixations (mean ± SEM) toward dog, human, item and letter images in dogs (Experiment II). Letters indicate statistically significant differences between image categories ($p < 0.05$).

In Experiment IV, paired samples t-tests were used to compare the proportional gazing times of object, background, head and body areas. Family and kennel dogs gazed at the head area longer than the body (0.10 ± 0.03 and -0.10 ± 0.03, respectively; $t_{23} = 3.3$, $p = 0.003$) or background area (0.10 ± 0.03 and -0.26 ± 0.03, respectively; $t_{23} = 8.6$, $p = 0.001$). In addition, the body area was gazed longer than the background area (-0.10 ± 0.03 and -0.26 ± 0.03, respectively; $t_{23} = 3.4$, $p = 0.002$). Furthermore, the object area was

gazed longer than the background area (0.27 ± 0.03 and -0.26 ± 0.03, respectively; $t_{23} = 8.3$, $p = 0.001$).

Experiment IV also showed that both dog groups gazed longer at the head area in wild animal images *versus* dog images (0.18 ± 0.04 and 0.06 ± 0.06, respectively; $t_{23} = -2.1$, $p = 0.050$, statistical trend) and likewise longer in wild animal *versus* human images (0.18 ± 0.04 and 0.07 ± 0.04, respectively; $t_{23} = -2.1$, $p = 0.043$). The body area was gazed longer in images containing dogs *versus* wild animals (-0.06 ± 0.06 and -0.18 ± 0.04, respectively; $t_{23} = 2.1$, $p = 0.050$, statistical trend), and also in images containing humans *versus* wild animals (-0.07 ± 0.04 and -0.18 ± 0.04, respectively; $t_{23} = 2.1$, $p = 0.043$). In addition, the background was gazed longer in images containing dogs *versus* wild animals (-0.22 ± 0.04 and -0.31 ± 0.03, respectively; $t_{23} = -2.1$, $p = 0.048$).

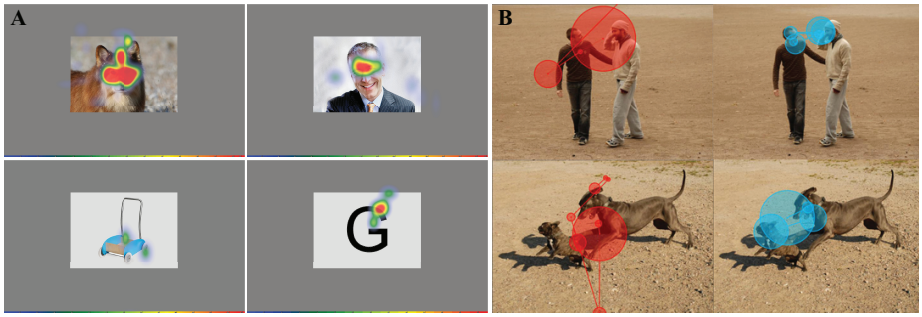

Figure 8 A) Examples of five dogs' averaged fixation durations towards Experiment II images (presented on gray background as in the real experiment) illustrated as heat maps. The dogs fixated the light blue areas the least (5 ms) and bright red areas the longest (100 ms or over). **B)** Example of one dog's (red color) and one human's (blue color) gazing toward human and dog social interaction images (Experiment III). Circles represent fixations (larger circle represent longer gazing time) and lines represent saccades (gaze transitions from one location to another).

5.3 DIFFERENCES BETWEEN HUMAN AND DOG VIEWING BEHAVIOR OF SOCIAL INTERACTION AND TWO DOG POPULATIONS LIVING IN DIFFERENT SOCIAL ENVIRONMENTS

Observations of conspecific and non-conspecific social interactions were compared between humans and dogs in Experiment III. Overall, both humans

and dogs gazed longer at the actors in social interactions than non-social images. However, dogs gazed longer at the actors in human rather than dog social interaction images and humans gazed longer at the actors in dog rather than human social interaction images (Table 4, Figure 8). The effect of social living environment was studied in experiments III and IV by comparing the gazing behavior of family and kennel dogs (Figure 9).

The gaze times of dog experts and non-experts were compared with repeated-measures ANOVA. The results of the ANOVA were further clarified with independent and paired samples t-tests. There was no difference in the image area gaze time between experts and non-experts ($F_{1,24} = 0.4$, $p = 0.5$), but a main effect of category was found ($F_{2,47} = 6.0$, $p < 0.01$). Both groups gazed longer at pixel images than human non-social (human_away) images (2313 ± 55 and 2110 ± 91 ms, respectively; $t_{25} = 3.4$, $p < 0.01$) and dog non-social (dog_away) images were gazed at longer than human_away images (2284 ± 67 and 2110 ± 91 ms, respectively; $t_{25} = 3.5$, $p < 0.01$). The gazing time of pixel images created from social images (toward) and pixel images created from non-social images (away) did not differ between experts and non-experts ($F_{1,24} = 0.4$, $p = 0.5$, repeated-measures ANOVA). In addition, the paired samples t-tests showed that across groups, the gazing times of toward and away pixel images did not differ (2341 ± 61 and 2307 ± 56 ms, respectively; $t_{25} = 1.0$, $p = 0.3$).

There was no difference in the relative gaze time of the object area between experts and non-experts ($F_{1,24} = 0.5$, $p = 0.5$), but main effects of species ($F_{1,24} = 12.3$, $p < 0.01$) and behavior ($F_{1,24} = 40.3$, $p < 0.001$) were found (Experiment III). Across groups, the object area was gazed relatively longer in human social interaction (human_toward) than human_away (68 ± 3.7 and 59 ± 2.9%, respectively; $t_{25} = 3.6$, $p < 0.01$), dog social interaction (dog_toward) than dog_away (77 ± 2.5 and 68 ± 2.3%, respectively; $t_{25} = 4.9$, $p < 0.001$), dog_toward than human_toward (77 ± 2.5 and 68 ± 3.7%, respectively; $t_{25} = 2.6$, $p < 0.05$) and dog_away than human_away images (68 ± 2.3 and 59 ± 2.9%, respectively; $t_{25} = 3.4$, $p < 0.01$). Between experts and non-experts, there was no difference in the number of saccades between objects ($F_{1,22} = 0.001$, $p = 0.9$). Nevertheless, a main effect of category was

found ($F_{2,42}$ = 6.2, p < 0.01). Across groups, humans displayed more saccades between objects in dog_toward than human_toward images (1.4 ± 0.07 and 0.9 ± 0.13, respectively; t_{23} = 3.6, p < 0.01), and in dog_away than human_away images (1.4 ± 0.07 and 1.1 ± 0.05, respectively; t_{23} =3.1, p < 0.01, Table 4).

The gaze times between family and kennel dogs were compared with the same statistical methods as in humans (repeated-measures ANOVA and t-tests). The image area gazing time differed between family and kennel dogs (between-subjects factor group, $F_{1,38}$ = 7.6, p < 0.01). In addition, there was a main effect of category ($F_{4,152}$ = 2.5, p < 0.05). Family dogs' image area gazing time was longer than kennel dogs in human_toward (1557 ± 83 and 1058 ± 119 ms, respectively; t_{38} = 2.8, p < 0.01), human_away (1544 ± 88 and 1056 ± 128 ms, respectively; t_{38} = 2.6, p < 0.05), dog_toward (1462 ± 92 and 929 ± 132 ms, respectively; t_{38} = 2.7, p < 0.05) and dog_away (1460 ± 79 and 930 ± 96 ms, respectively; t_{38} = 3.2, p < 0.01) categories, but gazing times did not differ in the pixel category (1441 ± 96 and 1070 ± 104 ms, respectively; t_{38} = 1.9, p = 0.07, Figure 9). In within groups comparisons, family dogs gazed at the image area longer in human_toward than pixel (t_{31} = 2.5, p < 0.05), human_away than pixel (t_{31} = 2.5, p < 0.05) and human_away than dog_away categories (t_{31} = 2.1, p < 0.05). In kennel dogs, the gazing time of the image area was longer in human_away than dog_away category (t_7 = 2.4, p < 0.05). In addition, there was no difference in the gazing time between toward and away pixel images for family and kennel dogs (between-subjects factor group, $F_{1,38}$ = 3.1, p = 0.08). Paired-samples t-tests showed that across groups, the gazing times of toward and away pixel images (1358 ± 94 and 1391 ± 84 ms, respectively; t_{39} = 0.5, p = 0.6) did not differ.

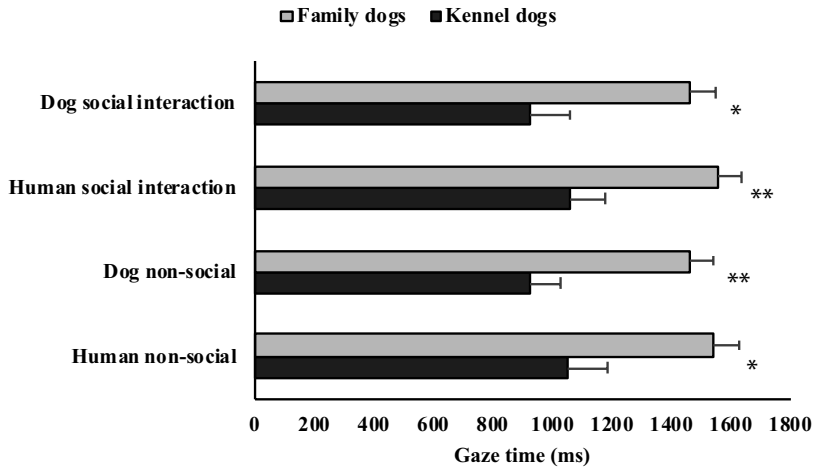

Figure 9 The differences between family and kennel dogs gazing times (mean ± SEM) toward stimulus images in Experiment III. Asterisks indicate statistically significant differences between dog groups (**p < 0.01 and *p < 0.05).

There was no difference in relative gazing time at the object area between family and kennel dogs ($F_{1,38}$ = 0.6, p = 0.5). Instead, species ($F_{1,38}$ = 7.1, p < 0.05) and behavior ($F_{1,38}$ = 22.2, p < 0.001) main effects were found. Both dog groups' relative gazing time was longer at the object area in interaction images and human images. The gaze time was longer in human_toward than human_away (42 ± 1.5 and 31 ± 1.8%, respectively; t_{39} = 5.9, p < 0.001), dog_toward than dog_away (36 ± 1.5 and 30 ± 1.4%, respectively; t_{39} = 4.9, p < 0.001) and human_toward than dog_toward (42 ± 1.5 and 36 ± 1.5%, respectively; t_{39} = 13.3, p < 0.001) images. In addition, between family and kennel dogs, there was no difference in the number of saccades between objects ($F_{1,22}$ = 4.1, p = 0.06), but a main effect of category was found ($F_{3,66}$ = 9.1, p < 0.001). Across groups, dogs demonstrated more saccades between objects in human_toward than in human_away images (0.2 ± 0.03 and 0.03 ± 0.01, respectively; t_{23} = 4.9, p < 0.001, Table 4).

Table 4 The relative gaze times (the gaze time (ms) of the object area divided by the gaze time (ms) of the image area in percentage ± SEM) of image categories by humans and dogs in Experiment III.

Image category	Relative gaze time (%) ± SEM.	
	Humans	Dogs
Human social interaction	68 ± 3.7	42 ± 1.5
Dog social interaction	77 ± 2.5	36 ± 1.5
Human non-social	59 ± 2.9	31 ± 1.8
Dog non-social	68 ± 2.3	30 ± 1.4

In Experiment IV, the proportional gazing times of object, background, head, and body areas of the images were compared between family and kennel dogs with repeated-measures ANOVA and the results were further clarified with paired samples t-tests. There was no difference in the proportional gaze time between family and kennel dogs (between-subjects factor *group*, $F_{1,22} = 0.024$, $p = 0.877$). Instead, main effect of *AOI area* ($F_{2,38} = 38.9$, $p = 0.001$) and interaction effects between *AOI area x group* ($F_{2,38} = 4.6$, $p = 0.020$), *AOI area x species* ($F_{3,62} = 2.9$, $p = 0.046$), *AOI area x image category* ($F_{3,69} = 10.1$, $p = 0.001$) and *AOI area x image category x group* ($F_{3,69} = 3.2$, $p = 0.028$) were found.

Family dogs gazed at the head area longer than the body (0.15 ± 0.03 and -0.15 ± 0.03, respectively; $t_{15} = 4.6$, $p = 0.001$) or background (0.15 ± 0.03 and -0.31 ± 0.04, respectively; $t_{15} = 11.0$, $p = 0.001$) areas. In addition, family dogs' gazing time was longer for the object area than for the background (0.31 ± 0.04 and -0.31 ± 0.04, respectively; $t_{15} = 8.0$, $p = 0.001$) area. Furthermore, the body area gazing time was longer than the background area gazing time (-0.15 ± 0.03 and -0.31 ± 0.04, respectively; $t_{15} = 2.7$, $p = 0.018$). In kennel dogs, the gazing time was longer for the head than the background (0.01 ± 0.05 and -0.18 ± 0.04, respectively; $t_7 = 3.3$, $p = 0.012$) area. In addition, kennel dogs' gazing time was longer for the object than the background area (0.18 ± 0.04 and -0.18 ± 0.04, $t_7 = 4.1$, $p = 0.005$).

In experiment IV it was also found that family dogs gazed longer at the head area in images containing a single human or animal *versus* paired human or animal (0.22 ± 0.06 and 0.07 ± 0.02, respectively; $t_{15} = 2.7$, $p = 0.017$).

Family dogs also gazed longer at the body area in paired *versus* single human or animal images (-0.07 ± 0.02 and -0.22 ± 0.06, respectively; $t_{15} = -2.7$, $p = 0.017$). Furthermore, family dogs gazed longer at objects in single human or animal *versus* landscape images (0.49 ± 0.08 and 0.11 ± 0.03, respectively; $t_{15} = -4.9$, $p = 0.001$) and likewise longer in paired human or animal *versus* landscape images (0.31 ± 0.06 and 0.11 ± 0.03, respectively; $t_{15} = -3.2$, $p = 0.007$) and also longer in single human or animal *versus* paired images (0.49 ± 0.08 and 0.31 ± 0.06, respectively; $t_{15} = 2.4$, $p = 0.030$). Instead, family dogs gazed longer at the background area in landscape *versus* single (-0.11 ± 0.03 and -0.49 ± 0.08, respectively; $t_{15} = 4.9$, $p = 0.001$) or paired images (-0.11 ± 0.03 and -0.28 ± 0.05, respectively; $t_{15} = 3.0$, $p = 0.010$). Likewise, they gazed longer at the background areas in paired *versus* single images (-0.28 ± 0.05 and -0.49 ± 0.08, respectively; $t_{15} = -3.5$, $p = 0.003$). In kennel dogs, the gazing times of object area were also longer for paired human or animal *versus* landscape images (0.29 ± 0.09 and 0.08 ± 0.06, respectively; $t_7 = -4.0$, $p = 0.005$). Kennel dogs also gazed longer at the background area in landscape *versus* paired human or animal images (-0.08 ± 0.06 and –0.26 ± 0.07, respectively; $t_7 = 3.5$, $p = 0.009$).

6 DISCUSSION

This thesis examined the feasibility of non-invasive EEG and eye tracking methods in studying dogs' neuronal functions and cognitive processes. This was investigated in studies that involved viewing different kinds of social and non-social stimulus images, comparisons of human and dog gazing behavior and by comparing two dog groups living in different social environments.

6.1 RELIABILITY OF NON-INVASIVE EEG IN DOG COGNITION STUDIES

Experiment I was designed to validate the feasibility of non-invasive EEG in alert non-medicated dogs by measuring the visual ERPs in individual dogs and within the group level. We detected the early visual N1 response of dogs at approximately 75 – 100 ms, which roughly corresponds with the visual N1 in humans. Compared to the typical human visual N1 response, which peaks around 100 ms, dogs' response occurred somewhat earlier, but otherwise the transient form of the ERP response was similar in both species. In addition, all individual dogs showed highly similar ERP responses peaking at approximately 100 ms ($p < 0.001$) within the lateral posterior channels, which are the channels closest to the occipital brain areas of primary visual processing (Van Essen 1979; Uemura 2015). This result validates the feasibility of non-invasive ERP measurements in individual dogs.

The earlier occurrence of the N1 response in dogs compared with humans is in accordance with non-human primate studies (Van der Marel et al. 1984; Woodman et al. 2007). In the Bichsel et al. (1988) study investigating anesthetized dogs, the mean latency of visual N1 response was approximately 54 – 56 ms recorded with subdermal electrodes. Methodological differences between human and animal studies can also lead to variations in results. Subdermal single-unit recordings tell us about the functional characteristics of individual neurons and non-invasive surface electrodes record large ensemble activity (Woodman et al. 2007). Anesthesia suppresses neural activity and

cerebral blood flow (*e.g.* Ueki et al. 1992; Sicard et al. 2003), and therefore studies on conscious animals reflect the brain activity under more real-life conditions. The early N1 response in dogs and monkeys may be related to their smaller brain size compared to humans: the smaller brain has fewer neurons and synapses, so the information transmission has less delay and is faster (Woodman et al. 2007). In addition, the tasks used may contribute to the visual N1 latency and amplitude (Mangun 1995). In this thesis, dogs passively observed the images (Experiment I), whereas commonly in similar human object perception studies a response is required, such as a button press (see *e.g.* Carmel and Bentin 2002). This makes comparisons between canine and human data obtained from these studies challenging. To date, all fMRI and EEG studies reported in dogs have used passive tasks where no behavioral response is required (for a review, Bunford et al. 2018), except one fMRI response inhibition study with a go/ no-go paradigm (Cook et al. 2016). Passive tasks have been preferred, because dog's movements during active behavioral response would cause major artifacts in the data.

Although the dogs participating in the EEG measurements were all purpose-bred beagles with similar skull size and formation, some individual variation was detected in the amplitude of the visual N1 response. Variation at the location of the channel that showed the maximum response between dogs was also apparent (Experiment I). Part of this variation may be explained by differences in the folding pattern of the cortex, which can affect the ERP components' cortical generator source location and orientation (Luck 2005). Additionally, other anatomical differences, such as brain and skull sizes and thickness of the head subcutaneous muscles may have led to differences in electrode placement, and variation in the maximum response location.

Compared to human EEG measurements, where the International 10 – 20 system is used to maintain the relative distances between electrodes constant (Jasper 1958), we have no standardized testing procedures for use in dogs. In a canine epilepsy study, James et al. (2017) used 15 subcutaneous needle electrodes that were placed in a similar pattern to human 10 – 20 system. However, canine and human skull morphology is not the same and therefore the electrode placement may also differ. Further differences between dog and

human measurements are the type and amount, of electrodes used. In humans, the EEG is usually measured non-invasively from the scalp, but in dogs, fully non-invasive measurements, where the dog is not sedated or anesthetized were not in existence before experiment I of this thesis.

Because dogs' fur is thicker than human hair, the placement and attachment of the electrodes (*e.g.* cup electrodes commonly used in humans) for dogs is challenging. Different kinds of electrodes were tested for dogs during the piloting phase of experiment I. Neonatal electrodes with bioadhesive gel and cloth were chosen for the experiment, because these electrodes were easiest to modify to the right size and to attach to the skin resulting in low impedances. While a human EEG head cap can have up to 200 electrodes, typically in dogs, measurements from one to 17 electrodes have been used (*e.g.* Bergamasco et al. 2003; Howell et al. 2012; Kujala et al 2013; Kis et al 2014). In our study (Experiment I), we used seven electrodes, the positions of which were visualized with respect to each dog's brains with CT imaging before the EEG measurements. CT images were used to find the optimal locations for the placement of the electrodes. There were differences in the head size and formation of the participating dogs, and especially in dogs with the smallest heads it was difficult to fit more than seven electrodes on to the surface of the dog's head.

In conclusion, the visual ERPs measured in experiment I confirmed that non-invasive EEG can be reliably used in intact fully alert dogs in cognition studies. As there were no standardized methods for EEG measurements in dogs at the time –which is also the case at present– we developed all of the procedures for the experiment I measurements. Training the dogs to stay still was necessary to be able to take measurements from animals that were not sedated or sleeping. This is because movement causes major artifacts and loss of data in both EEG and eye tracking studies.

6.2 VISUAL EVENT-RELATED POTENTIALS DURING HUMAN AND DOG FACIAL IMAGE VIEWING IN DOGS

The early visual ERP responses differed between human and dog facial images at 75 – 100 ms at the group level in the posterior sensor P3 (Experiment I). This difference was detected within the transient, early visual N1-like response. However, early ERPs are sensitive to low-level differences in the stimulus images, and it is possible that the early differences were due to elementary stimulus features such as luminance and contrast, that were not specifically matched across categories. Showing dark compared to bright stimuli against similar backgrounds elicits larger amplitude and delayed peak latency of the N1 component in humans (Hughes et al. 1984; Johannes et al. 1995; Wijers et al 1997). Dogs' abilities to discriminate differences in brightness have been estimated to be half that of humans (Pretterer et al. 2004; Kasparson et al. 2013). In Experiment I, this may have affected dogs' perception of the stimulus images and the related ERP responses. In Experiment I, dog facial images were overall darker than human facial images, because of the different coat colors and patterns the dogs presented in the images. This might have also influenced the observed ERP differences between image categories. This should be taken into account in future studies, where early visual responses are the focus of the study.

Later differences in visual ERP responses between human and canine facial images were also detected at the group-level data in an electrode located anterio-laterally on the left side of the dog's head, above the dog's temporal cortex. The temporal cortex is associated with visual processing of faces in humans (Allison et al. 1994; Puce et al. 1995; Kanwisher and Yovel 2006), in monkeys (Gross et al. 1972; Perrett et al. 1982; Tsao et al. 2006) and in sheep (Kendrick and Baldwin 1987; Kendrick 1991). The later ERP responses are considered to be quite unaffected to contrast changes (*e.g.* Rolls and Baylis 1986; Avidan et al. 2002). However, EEG recordings are highly sensitive to artifacts, such as eye and muscle movements, which can be difficult to distinguish from true cerebral activity (Libenson 2010). As there were no clear brain responses within this late time window, artifacts may have

also affected the results of Experiment I and therefore replication is needed to confirm these results. In the Experiment I, only face stimuli were used, but in the future studies also other stimulus categories should be included to be able to compare visual ERP responses for example between faces and objects (Dilks et al. 2015). Recent fMRI studies have confirmed that likewise, dogs have brain regions in the temporal lobe specialized for the processing of faces (Dilks et al. 2015; Cuaya et al. 2016). Nevertheless, differences between canine and human brain structures make it difficult to determine if a measured electrocortical signal derives from comparable populations of neurons (for a review, Bunford et al. 2017).

The results showed differences in earlier and later ERPs to dog and human face images, but more studies are still needed to confirm these results, since this was the first study using non-invasive EEG measurement in dogs. At this point, we cannot exclude the possible effects of low-level stimulus properties or some unaccounted-for artifacts in the ERP responses, even after the rather rigorous data cleaning and artifact removal.

6.3 RELIABILITY OF EYE TRACKING IN DOG COGNITION STUDIES

This thesis examined the applicability of eye tracking for dog cognition studies (Experiments II – IV), and also for direct comparisons between dogs and humans (Experiment III). The eye tracker that we utilized in our studies is designed for humans, and therefore it is not optimal for dog studies. Eye-tracking systems use an eye movement detection algorithm and threshold settings for categorizing the raw eye movement data into fixations and saccades. The default settings are developed for tracking adult human eyes, and if dogs' eye movements differ from humans', the algorithm may not work in an optimal way (Park et al. 2020). Despite this limitation, calibration accuracy was sufficiently high in all experiments (on average 91.7 %) and eye tracking data were successfully collected from almost all of the participating dogs.

In experiments II – IV, dogs' binocular eye movements were recorded and averaged. In experiment III, monocular eye tracking was used in humans. Holmqvist et al. (2011) reported that usually human participants' eyes look at the same position, but some people have one dominant and one passive eye, which looks in a different direction. Similar differences may also exist between dogs' eyes, and therefore using monocular eye tracking might give more precise results. Binocular eye tracking was used in our experiments, because the eye tracker we used was designed for binocular eye tracking and the calibration was made with both of the dogs' eyes. In experiments II – IV the eye tracker was calibrated using a five-point procedure, where the screen was replaced with a plywood wall with five holes in the calibration point positions, and the experimenter showed a treat in the hole to attract the dog's attention. This calibration method was developed in experiment II, because there was no previous calibration method for use in dogs. It would have been difficult to get dogs to look at the calibration points presented in the display without training them to look at those points.

Experiments II – IV participants included dogs of multiple breeds. They had varying head shapes and respectively, their eyes were at varying angles with respect to the eye tracker, which might have affected how well the eye tracker could measure the eye gaze. In experiment II, where the tracking ratio (mean percentage of the time eye tracker could detect a pupil) was reported, the eye tracking succeeded better for one eye than the other. In dogs with long muzzles/ snouts, the snout can obscure the eyes, such that the infrared rays sent by the eye tracker could not reach both of the dog's eyes. Therefore, each dog's eyes had to be individually calibrated for the eye tracker and dog position optimally adjusted for the measurements.

Based on these eye tracking experiments it was concluded that measuring dogs' eye movements is challenging, but possible. Measuring dogs' cognitive functions with eye tracking can provide details that cannot be seen from the dogs' behavior. In addition, comparisons with results in humans can be done using the same paradigm in both species. However, the default eye movement classification algorithms of human eye trackers, may not be optimal for dogs, and this should be considered in future studies.

6.4 ATTENTIONAL FOCUS ON THE PRESENTED IMAGES IN DOGS

Eye gaze tracking demonstrated that dogs were looking more at the monitor when images were displayed than when the monitor was blank (Experiment II). This indicates that dogs did not learn to fixate on the monitor merely in anticipation of a reward even when images were not presented. Dogs were also focusing their attention on the images' informative regions, such as the face and the whole-body area, without specific training for this kind of targeting (Experiments II–IV). This result has been further confirmed in other canine eye tracking studies (*e.g.* Téglas et al. 2012; Somppi et al. 2014; Barber et al. 2016). However, dogs do not maintain a constant level of attention on the stimuli, particularly if the same images are repeated. The first frame of the image series attracted the highest looking time, and the looking time was decreased when the image was repeated (Experiment II). Visual habituation (decline in looking with repeated presentation of stimulus) is a well-known psychological effect (Fantz 1964), which has been widely studied in human infants (for a review, Colombo and Mitchell 2009). Consistently, it has been also found in monkeys (Joseph et al. 2006) and our result was verified in another recent canine study (Kis et al. 2017b). These results confirm that dogs' basic cognitive processes (*e.g.* habituation) during image viewing are similar to humans', because similar processes have been found also in human eye tracking studies.

Dogs were also found to gaze at images for a shorter time than humans (Experiment III). This finding suggests that dogs have quicker processing mechanisms, *i.e.* they need less time to decode the social cues. Dogs also might have a more limited attention span, or they are more easily bored than adult humans (see for a review, Wróbel 2000; Burn 2017). Based on our experiments, it is hard to define an optimal presentation time of the images or the length of image series for the dogs. Video clips with moving targets might hold dogs' attention better than still images, because dogs' visual system is especially adapted to following movement (Miller and Murphy 1995). In addition, the ecological validity of videos might be better than still images, but the analysis of complex video stimuli is not straightforward. Contrary to our

results and other studies where human and dog gazing behavior have been compared (Guo et al. 2009; Racca et al. 2012; Correia-Caeiro et al. 2020), a recent eye-tracking experiment suggest that dogs' saccades/ eye movements are slower and fixations longer than those of humans for facial or round non-facial objects (Park et al. 2020). However, the total gaze time was not reported in the work by Park and colleagues (2020). Longer fixations might be beneficial for the dog, whose visual system is especially adapted to following movement. Longer fixations make it possible to keep their sight focused on moving objects or focused on motionless objects when the dog is moving (Sjaastad et al. 2010). The discrepancy between study results might be due to the different kind of stimuli (natural full-body versus close-up facial images) or differences in the eye tracking systems' sampling frequencies and algorithms used (Holmqvist et al. 2011; Park et al. 2020).

Dogs focused their gaze on the biologically relevant and informative areas of the images. In Experiment II, where faces, items and letters were shown, dogs fixated longer on the image compared with the surrounding background monitor area and on the object compared with the image background. Similarly, in Experiment IV, where animals and humans were shown in different kinds of natural backgrounds, dogs gazed at the living creatures (object area) longer than background area of the images, as previously reported in humans and non-human primates (*e.g.* Yarbus 1967; Nahm et al. 1997; Kano and Tomonaga 2009). Experiment IV results suggest rapid and accurate detection of living creatures from landscape images by dogs, which have been previously shown in humans and non-human primates (*e.g.* Fabre-Thorpe et al. 1998; Thorpe et al. 2001). Dogs' focus on the biologically relevant information is also consistent with the "life detector mechanism" (for a review, Rosa Salva et al. 2015). In addition, dogs generally gazed longer on the head than the background area, which highlights the importance of faces in visual processing of social animals (for a review, Leopold and Rhodes 2010).

In conclusion, dogs focused their attention on the presented images and biologically relevant areas in them (Experiments II-IV). Compared to humans, dogs gazed at images for a shorter time, which can be related to dogs' quicker processing mechanisms or limited attention span. However, to differentiate

between these two, more comparative studies are needed, where dogs' and humans' eye movements are measured under similar conditions.

6.5 EFFECTS OF IMAGE CATEGORY AND COMPOSITION TO THE GAZING BEHAVIOR IN DOGS

In Experiments II and III, dogs' gazing times differed between image categories, which suggests that dogs can differentiate images based on their categorical content. These findings are in accordance with earlier behavioral studies, where dogs have been explicitly taught to discriminate between image categories (Range et al. 2008; Autier-Dérian et al. 2013), and also with other eye tracking studies in dogs (Somppi et al. 2014, 2016, 2017; Barber et al. 2016).

Relatively little is known about the basic visual capacities of dogs, and yet most of the cognitive research tasks in dogs are visual, because these tasks are adapted from human and monkey studies (for a review, Byosiere et al. 2018). Based on the findings in experiments I – IV, dogs can differentiate the image categories and concentrate their eye movements on the informative areas of the images, but how they actually perceive these images remains a mystery. Dogs' visual acuity seems to be less precise, and also brightness discrimination and color vision are more limited than in humans. Estimates of dogs' visual acuity have varied greatly probably owing to various research methods (*e.g.* Odom et al. 1983; Miller and Murphy 1995; Tanaka et al. 2000a; Lind et al. 2017), so there is a need to develop a reliable visual acuity measure to assess which size of stimuli dogs are able to see clearly. Variation in head and facial morphology (muzzle length, skull shape) between dog breeds may affect the eye structure (McGreevy et al. 2004), visual acuity (Murphy et al. 1992; for a review, Byosiere et al. 2018) and also the cognitive performance (Gácsi et al. 2009b). The differences between the visual capacities of different dog breeds will provide an excellent topic for a further study.

In experiments I – IV, dogs were shown color images of humans, animals, letters of the alphabet, and items. In previous canine studies both gray-scale images and color images were used (*e.g.* Range et al. 2008; Racca et al.

2012). Dogs' color discrimination abilities remain controversial (*e.g*. Neitz et al. 1989; for a review, Byosiere et al. 2018), and it is unclear how dogs perceive these images. Kasparson et al. (2013) suggests that color cues are more important than brightness when dogs are choosing between stimuli; color can be one of the characteristics that enable the discrimination and recognition processes. However, stimulus images have been quite simple in studies where dogs' perceptual abilities have been tested, and it is not the natural situation, where objects and events generate complex stimuli that affect several senses (Miklósi 2014). By developing more natural tasks and experimental situations we could obtain more valid data from comparative studies between humans and dogs (Cook 1993; Hare 2001; Stevens 2010).

Composition of the images can affect the dogs gazing behavior. In the experiments of this thesis, different kinds of stimulus images were used, which can create discrepancies in the results. In Experiment II, dogs gazed at canine facial images more than human facial images, but in Experiment III, where full body images of social interaction were used, they gazed at humans more than dogs. In addition, the size of the object in the image can affect the gazing behavior. In Experiment IV, dogs gazed less time at animals/ humans in landscape images, in which the size of the object was smaller relative to the background, than in other types of images. Reduced looking times of smaller objects in Experiment IV suggests that dogs are not able to see small differences in the images, which may be related to poorer visual acuity and less ability to distinguish brightness in dogs than in humans (Pongracz et al. 2017; for a review, Byosiere et al. 2018). However, one of the reasons for the reduced looking times of smaller objects might be that the calibration accuracy was not sufficient for the smaller objects in these images. Dogs might have actually looked at these objects, but the accuracy of the eye tracker was not sufficient to detect the gazes with this precision.

Thus, the results of these experiments indicate that dogs are able to spontaneously differentiate images based on their categorical content. However, there is still a lack of basic information on dogs' visual abilities and what size of objects dogs are able to distinguish from the images.

6.6 THE DIFFERENCES BETWEEN DOGS' AND HUMANS' GAZING BEHAVIOR IN IMAGES WITH SOCIAL AND NON-SOCIAL CONTENT

This thesis examined visual processing of different kinds of stimulus images by dogs, varying also in their social content. In Experiment III, the gazing behavior of humans and dogs were compared to social and non-social images. In the studies of thesis, dogs gazed at canine facial images more than human facial images (Experiment II), but when dogs gazed at full body images of social interaction, they gazed at humans more than dogs (Experiment III). In addition, humans gazed longer at the actors in canine rather than human interaction images (Experiment III). This suggests that processing of non-conspecific social interactions may take more time and be cognitively more demanding for both dogs and humans. Furthermore, dogs and humans might use an adaptive social attention strategy, which is influenced by innate preferences, social learning and experiences. Dogs' gazing behavior towards human social interaction images might also reflect their inherent sensitivity to human social gestures (Udell et al. 2010).

Images in Experiments II and III were contextually quite different (large close-up faces versus full body images from the side view at a greater distance), which may partly explain the differences in dogs' gazing behavior between these experiments. It might be that close-up facial images of conspecifics were more threatening and drew dogs' attention more than full body images from the side view. In experiment II, dogs might have looked at dog faces more than human faces, because they were biologically more relevant and therefore captured their attention more effectively. It is also possible that dogs avoided gazing directly at human faces, even though the facial images in this study were neutral. During domestication, dogs might have adapted to living with humans by displaying such conflict-avoiding signals towards humans (Győri et al. 2010; Somppi et al. 2016).

When results from dogs and humans were compared in Experiment III, similarities were also found. Both dogs and humans gazed longer and made more transitions (saccades) between actors in social interaction rather than non-social images. In social interaction situations both faces and whole bodies

are important sources of information because facial expressions, bodily gestures and postures reflect the emotional states and goals of actors. In the previous fMRI study, similar brain areas related to social cognition were activated when humans observed humans or dogs in interactional situations, suggesting similarities in brain mechanisms processing social information regardless of species (Kujala et al. 2012). In dogs, social interaction stimuli have not been studied yet, but a recent dog fMRI study found a temporal lobe area that responded similarly to human and dog face images (Dilks et al. 2015; but see Thompkins et al. 2018). Direct comparisons between humans' and dogs' cognitive functions are still very rare, which is probably due to the tradition of comparing humans and non-human primates and a lack of methods, that allow direct comparisons. Non-invasive EEG and eye tracking make comparisons possible, as well as fMRI technique, but they require the dogs to be trained to stay in place during the measurements.

In experiments II - IV, the differences between image categories imply, that dogs can differentiate social and non-social stimuli from each other, and that they preferred to look at the stimuli that were more socially and biologically relevant for them. Differences between social interaction and non-social images of Experiment III are unlikely to be due to responses to low-level stimulus properties (*e.g.* contrast and luminance). This is because gazing times of the pixelated stimulus images, manufactured from the interactive and non-interactive images, differed neither in humans nor in dogs.

To summarize, differences and also similarities were found between humans and dogs gazing behavior towards social stimuli. Both dogs and humans gazed for longer at social stimuli than at non-social stimuli. However, both species gazed for longer at actors in non-conspecific images, which might indicate that the processing of social interaction of non-conspecifics is more demanding.

6.7 GAZING BEHAVIOR OF TWO DOG POPULATIONS LIVING IN DIFFERENT SOCIAL ENVIRONMENTS

This thesis also investigated the effect of social environment and life experiences on the gazing behavior of two dog groups: family and kennel dogs. Family dogs live closely and interact constantly with humans, whereas kennel dogs usually live in quite isolated kennel facilities and interact more with their own small group of dogs than with humans. Topál et al. (1997) showed, that dogs kept outside of the house (*e.g.* as guard dogs) used less gazing behavior towards human in a problem-solving task than dogs that were kept indoors for companionship.

In this thesis, family dogs gazed at social images (interacting dogs or humans) longer than kennel dogs that were living in a limited social environment, but otherwise their gazing behavior did not differ (Experiment III). This suggests that social experiences might have affected the processing of the social stimuli, but that the basic processing of social stimuli is similar despite social experiences. During domestication, dogs may have been predisposed to detect human social cues, but also the exposure to humans affects how social information is processed (for a review, Reid 2009). In Experiment IV, family dogs focused their gaze at the head areas of single animals or humans, but in images containing paired animals or humans, they gazed more at the body than the head areas. Family dogs' fixations may have been spread more widely in images containing two head areas i.e. in the paired than in the single animal or human images. In these images, the social bodily gestures (two animals or humans sitting or standing close to each other) may have drawn family dogs' attention into body areas. Kennel dogs' gazing times did not differ between head and body areas in the single or paired images. Otherwise family and kennel dogs gazing behavior was quite similar. Consistently with Experiment III and IV results, a recent behavioral study showed that kennel dogs were less responsive/ active to social and environmental stimuli than family dogs or kennel dogs that were adopted at age of 8 weeks of age by families (Turcsán et al. 2020). Experiment III and IV results are also consistent with another eye tracking study of our research group, where kennel dogs gazed at faces for a shorter duration of time than

family dogs did (Somppi et al. 2014). However, in another study, the total looking time at human faces was longer in kennel dogs than family dogs. This study suggests that it takes longer for kennel dogs to process the facial information than family dogs, because kennel dogs have less experience of faces as they are not part of their daily visual environment (Barber et al. 2016). The discrepancy between results might be affected by the different kind of stimuli, testing procedures and data analysis used in these experiments.

In addition, breed can affect dogs' viewing behavior. Previous behavioral studies have shown, that herding and working dogs that have been bred to respond to human communicative signals, are more skilled at using gestural cues. They show more human-directed gazing behavior than dogs that are not bred for cooperation with humans, *e.g*. primitive and molossoid dogs (Wobber et al. 2009; Passalacqua et al. 2011). Kennel dogs that participated in the experiments of this thesis were beagles, which are hunting dogs bred for more independent hunting than cooperation with humans, and most of the family dogs were breeds from herding or working groups. However, there might be great individual variation within dog breeds, which should also be considered in future studies (Arden et al. 2016; Turcsán et al. 2020). In addition, dogs' sociability and training level can affect their willingness to gaze at social images or read social gestures in behavioral tests (Jakovcevic et al. 2012; Marshall-Pescini et al. 2009; McKinley and Sambrook 2000). Kennel dogs were quite fearful and cautious in training and experimental situations compared to family dogs, and it took more time for kennel dogs to learn for example to keep their heads on the chin rest. Most of family dogs had also had previous training experience from obedience, agility, or other dog sports, which kennel dogs did not have.

Overall, the number of dogs participating in the experiments should have been higher to allow comparisons between dog breeds (Experiments III – IV). There was also a significant overlap in the dogs, which participated in the experiments. Therefore, our results might not be generalizable to the larger population comprising all existing dog breeds (for a review, Bensky et al. 2013; Arden et al. 2016). The reasons behind this might be the limited number of dogs available for studies, the prolonged training needed before the

experiments, and also dog owners' willingness to participate in multiple studies.

Thus, the results obtained in this thesis suggest that there are some differences in the gazing behavior between family and kennel dogs inferring the effect of social environment, but the basic visual processes seem to be similar between these dog groups. There are some discrepancies in the study results, which may be related to different study setups.

6.8 METHODOLOGICAL CONSIDERATIONS

In this thesis, novel non-invasive methods were developed for studying dogs' cognitive processes, and there is always a chance to improve things. Dogs were trained with positive operant conditioning method to lie still during the EEG and eye tracking measurements (Experiments I – IV) to prevent head movements, which cause major artifacts in data. Most of the excluded data in both EEG and eye tracking were due to a dog leaving or lifting its head from the chin rest. Dogs were trained to lie still, but they were not under any command, and they were free to move. Movement artifacts may be smaller when measuring EEG during sleep or drowsiness (*e.g*. Kis et al. 2017a), but this makes studying cognitive functions impossible. A fMRI study compared awake and lightly sedated dogs' brain responses to different odors and concluded that higher order brain structures responsible for cognitive functions were mainly activated only in conscious dogs (Jia et al. 2014). Recently, an eye tracking system has been developed that allow participants to move more freely by allowing more data noise (Correia-Caeiro et al. 2020).

Some studies suggest that intensive training of the dogs to the task might influence their natural responses, gazing patterns as well as their cognitive processes during image viewing (Kis et al. 2017b; Correia-Caeiro et al. 2020), although dogs were not trained to gaze at the images or monitor. In this thesis work, training was regarded as necessary because dog's movements during the calibration and eye tracking caused serious artifacts and loss of data, thus exposing studies to too few samples per dog. Movement artifacts are one of the reasons why extensive training has been very successfully also used in

fMRI studies with dogs (*e.g.* Berns et al. 2012). Furthermore, as dogs learn very quickly, they may also learn some behavior during the experiment, thus unwanted and unsupervised dog learning in the experimental studies pose a serious confounding factor since it is unaccounted for. In the future, this issue should be investigated further by comparing dogs that are trained to the task with untrained dogs.

It could be argued that it would be more natural to use odors for testing dogs' cognitive abilities rather than visual stimuli, because the sense of smell is highly important to dogs. Dogs' olfactory bulb and cortex are larger in size compared to humans, and the dog nose epithelium has hundreds of millions more olfactory cells than the human nose. Dogs' olfactory capability is at least 100 times greater for detecting certain odors than humans (Moulton et al. 1960; Gazit and Terkel 2003; Lindsay 2013). However, dogs also use their sight in everyday communication and based on the results of Experiments II – IV, they seem to pay attention to visual stimuli and are able to acquire social information from the still images by using only their sight.

6.9 FUTURE RESEARCH

Eye tracking and non-invasive EEG are promising methods for dog cognition studies, and with these methods we can advance our understanding of dog-human interaction and dog behavior. In the future, combining eye gaze tracking with EEG recording could show what is happening in the brain during a particular visual task. Simultaneous recordings could help to identify and reject eye movement artifacts (*e.g*. blinks) from the EEG signal (Plöchl et al. 2012). However, eye tracking and EEG recordings should be synchronized carefully, for example by sending marker signals into both data streams. Interesting new non-invasive methods in dog research are functional near-infrared spectroscopy (fNIRS) and infrared thermography (IRT). fNIRS was piloted in one study, where hemodynamic changes in canine brains during positive interactions with humans were measured (Gygax et al. 2015). IRT can be used to visualize and measure superficial temperatures and temperature changes in the body, that are related to illnesses, and also to stress and

emotional states (for a review, Stewart et al. 2005; Nakayama et al 2005; Vainionpää 2014).

For clinical purposes EEG has primarily been used in the diagnosis of canine epilepsy (*e.g.* Pellegrino and Sica 2004; Jeserevics et al. 2007; Jokinen et al. 2007). In the future, EEG and eye gaze tracking could be used to unveil the neurocognitive changes present in family dogs suffering from chronic pain (*e.g*. due to osteoarthritis). Identifying the effect of pain in animals is challenging (for a review, Hansen 2003; Vainio 2012; for a review, Reid et al. 2018), and new methods should thus be introduced. Given their evolutionary history with humans, dogs can be used as translational models for human disorders such as genetic diseases and age-related cognitive decline (Shearin and Ostrander 2010; Chapagain et al. 2018). Family dogs can be also monitored in their natural environment, which they share with humans, unlike laboratory raised monkeys or rats (for a review, Bunford et al. 2017).

The dog as a model can expand our understanding of human cognition and its evolution and may prove valuable in identifying mechanisms underlying human diseases. Furthermore, dog owners benefit from a better understanding of their dog's social-cognitive skills, which can improve welfare in dogs and cooperation between dogs and humans.

7 CONCLUSIONS

1. The feasibility of non-invasive EEG in dog cognition studies was confirmed. Early visual ERPs were detected in response to viewing facial images, and a difference between human and canine facial images was found, which may be associated with the visual processing of facial information.

2. Eye tracking is a promising method for studying canine cognitive abilities and also for comparing eye movements between humans and dogs. Dogs focused their attention on biologically relevant areas, such as head area, in the images presented.

3. Dogs' gazing times differed between image categories, which implies that dogs were able to differentiate between images according to their categorical content. In addition, the composition of the images affected dogs' gazing behavior, for example smaller objects were gazed at less than larger ones in the images.

4. Both humans and dogs gazed at social interaction images more than non-social images, but both gazed more at the other's species interaction than their own species.

5. Gazing behavior of two dog populations (family and kennel dogs) had minor differences. Kennel dogs that were living in a limited social environment gazed at social interaction images less than family dogs and focused their attention on different areas in the images, but otherwise the basic visual processes seem to be similar between family and kennel dogs.

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